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VOLUME 33 JUNE 1955 NUMBER 3

ORNITHOFILARIA ALGONQUINENSIS N. SP. FROM *HIRUNDO ERYTHROGASTER* WITH A REVISION OF THE GENERA *PARAMICIPSELLA* CHOW, 1939 EMEND. CHABAUD AND CHOQUET, 1953 AND *ORNITHOFILARIA* GÖNNERT, 1937[1]

BY ROY C. ANDERSON

Abstract

Ornithofilaria algonquinensis n. sp. is described from the barn swallow (*Hirundo erythrogaster*). Three species are recognized in the genus *Paramicipsella* Chow, 1939, namely: *P. brevicaudata* Chow, 1939; *P. lepidogrammi* (Tubangui and Masiluñgan, 1937) Chabaud and Choquet, 1953; *P. australis* (Johnston and Mawson, 1942) Chabaud and Choquet, 1953. The following species are recognized in *Ornithofilaria* Gönnert, 1937: *O. mavis* (Leiper, 1909) Gönnert, 1937; *O. travassosi* (Koroliowa, 1926) n. comb.; *O. stantschinskyi* (Gilbert, 1930) n. comb.; *O. lienalis* (Orloff, 1947) n. comb.; *O. brevispiculum* (Singh, 1949) n. comb.; *O. fallisensis* Anderson, 1954; *O. algonquinensis* n. sp.

Introduction

For a number of years it has been the practice of the members of the Wildlife Research Station in Algonquin Park, Ont., to capture and band adult barn swallows which nest in the abandoned buildings of an old lumber mill nearby. Blood smears were taken from the captured birds and microfilariae were found on a few of these. In 1953 one adult male swallow was accidently killed. Microfilariae were found in the blood and adult worms in the left pulmonary artery. This species is apparently new and is described herein as *Ornithofilaria algonquinensis* n. sp.

Ornithofilaria algonquinensis n. sp.

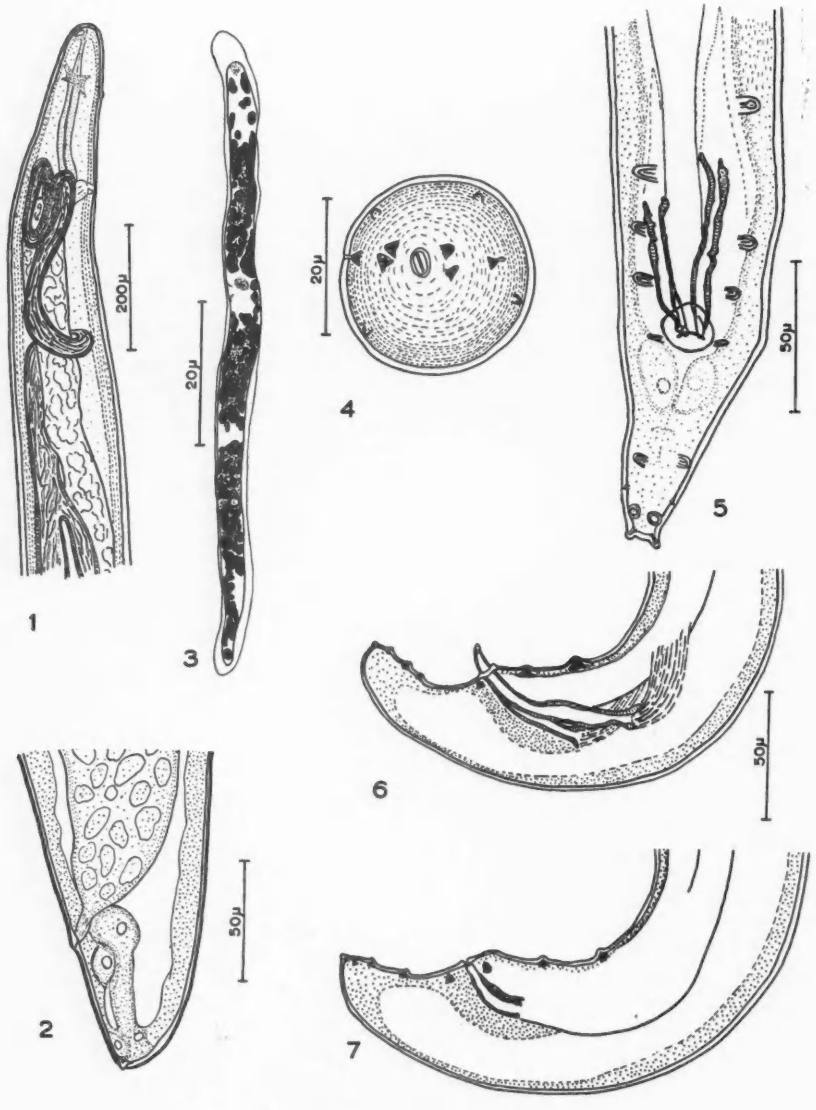
(Figs. 1–7)

Description

Dipetalonematidae Wehr, 1935 (14); Splendidofilariinae Chabaud and Choquet, 1953 (2). Small worms tapering markedly at the extremities. Oral opening a dorsoventral slit bordered by delicate, circumoral, cuticular ring. Oral papillae consisting of four pairs of submedian papillae. Amphids lateral.

[1] *Manuscript received January 25, 1955.*
Contribution from the Department of Parasitology, Ontario Research Foundation, and the University of Toronto, Toronto, Ontario.

[The April number of this Journal (Can. J. Zoology, 33 : 75-106. 1955) was issued April 7, 1955.]



FIGS. 1–7. *Ornithofilaria algonquinensis* n. sp.

FIG. 1. Anterior end female, dorsal view (allotype). FIG. 2. Tail end female, lateral view (allotype). FIG. 3. Microfilaria from blood, Giemsa stain. FIG. 4. Anterior end female, *en face* view (paratype female No. 3). FIG. 5. Tail end male, ventral view (paratype male No. 3). FIG. 6. Tail end male, lateral view (holotype). FIG. 7. Tail end of abnormal male, lateral view (paratype male No. 2).

Esophagus not divided externally into two parts. Intestine broad and transparent. Cuticle with delicate transverse striations about one micron apart.

Male (*Three Specimens*)

Length 11.9 (9.7, 9.4) mm.[2] Tail coiled. Head width 0.029 (0.026, 0.037) mm. Width of body at nerve ring 0.069 (0.058, 0.063) mm.; at anus 0.039 (0.040, 0.045) mm. Maximum width 0.12 (0.084, 0.14) mm., attained near middle of body. Nerve ring 0.090 (0.092, 0.079) mm. from anterior end. Excretory pore 0.106 (—, 0.092) mm. from anterior end. Esophagus 0.53 (0.70, 0.59) mm. long. Maximum width of esophagus 0.018 mm. Intestine, about 0.039 mm. in diameter, thin-walled, and transparent. Spicules subequal and slightly different morphologically, right 0.058 (0.031, 0.052) mm. long, left 0.080 (0.029, 0.063) mm. long (the spicules in the male paratype No. 1 are very short (Fig. 7) but as the muscles, usually attached to the proximal ends of the spicules, are absent, the writer concludes that the spicules are abnormal; the worm is otherwise similar to the holotype). Caudal papillae prominent and conical consisting of 2 (2, 3) pairs of preanal papillae, often slightly asymmetrically arranged, and 3 (2, 3) pairs of postanal papillae, one pair of which may be adanal in position. Tail provided with two prominent terminal protuberances. Phasmids lateral in position, about 10μ from tip of tail (Fig. 5). Anus a crescent-shaped slit surrounded by a slightly raised cuticular plate, 0.042 (0.047, 0.058) mm. from the tail end.

Female (*Two Specimens*)

Length, 22.5, 22.6 mm.[3] Width of head 0.042, 0.034 mm. Width of body at nerve ring 0.076, 0.066 mm.; at anus, 0.049, 0.048 mm. Maximum width of body 0.20, 0.17 mm., attained near middle of worm. Nerve ring 0.084 mm. from anterior end. Excretory pore 0.11, 0.10 mm. from anterior end. Esophagus 0.58 mm. long; maximum width 0.024, 0.018 mm. Intestine 0.066, 0.063 mm. broad. Tail 0.050, 0.066 mm. long, bluntly pointed, with pair of small terminal protuberances. Rectum short. Anus on slightly raised protuberance. Vulva 0.26, 0.21 mm. from anterior end, not opening on prominent protuberance. Vagina convoluted, 0.86, 0.42 mm. long, dividing into two opisthodelphic uteri. Vagina and uteri full of microfilarioid embryos, 76–84 (80) μ long. Eggs in posterior reaches of the uteri 16 $\times$ 20 μ in size, with an extremely fine oval envelope.

Microfilaria (*10 Specimens, Giemsa-stained*)

Short and stout with delicate transparent sheath extending slightly beyond extremities. Anterior end rounded, without cephalic space. Posterior end gently tapering to short blunt tail. Inner body prominent. Nuclear column composed of three or four rows of round to oval nuclei. Length of microfilaria 61–77 (70) μ. Relative positions of fixed points as follows: nerve ring 26%;

[2] *The first figure is from the holotype, the remainder from male paratypes 1 and 2 respectively.*
[3] *The first figure from allotype, the other from paratype female No. 2.*

excretory pore 32–39 (34)%; excretory cell 36–41 (39)%; anterior border of inner body 55–63 (59)%; posterior border of inner body 62–69 (64)%; first rectal cell 67%; anal pore 84–87 (85)%.

Host.—Barn swallow (*Hirundo erythrogaster* Boddaert).

Location.—Left pulmonary artery; microfilariae in the blood.

Locality.—Algonquin Park, Ontario, Canada.

Specimens.—U.S. Bureau of Animal Industry. No. 37444 (types).

Discussion

A few months ago the writer (1) expressed dissatisfaction with the revision of the genus *Paramicipsella* Chow, 1939 (4) proposed by Chabaud and Choquet (2). The substance of the criticism was that *Paramicipsella brevicaudata* Chow, 1939, which possesses a cuticular shield at the anterior end, was associated in the same genus with other species which lack this structure. In addition the emended *Paramicipsella* included species in which both spicules are identical and other species in which the spicules are subequal and morphologically dissimilar. The genus *Ornithofilaria* Gönnert, 1937 (6), moreover, was unsatisfactorily separated from the emended *Paramicipsella*. The writer and Dr. Alain Chabaud in recent correspondence have attempted to correct the deficiencies of the classification of Chabaud and Choquet (2) and through the courtesy of Dr. Chabaud it is possible to present here a revised dichotomy to replace that in their classification (2). The revised dichotomy is as follows:

10–(9) Queue courte

11–(14) Vulve au niveau de l'oesophage

12–(13) Tête généralement pourvue d'un bouclier céphalique. Spicules égaux et semblables.....*Paramicipsella* Chow, 1939

13–(12) Tête dépourvue de bouclier céphalique. Spicules subégaux .....*Ornithofilaria* Gönnert, 1937.

It is proposed to retain in the genus *Paramicipsella* the following species: *P. brevicaudata* Chow, 1939 (4); *P. lepidogrammi* (Tubangui and Masiluñgan, 1937) Chabaud and Choquet, 1953 (13, 2); *P. australis* (Johnston and Mawson, 1942) Chabaud and Choquet, 1953 (7, 2).

P. brevicaudata possesses a cephalic shield and the illustration of the anterior end of the closely related species *P. lepidogrammi* leads one to believe that this species likewise possesses this structure. A cuticular shield has not been described for *P. australis* but because of important similarities to *P. brevicaudata* the writer, along with Dr. Chabaud, believes that it should be retained in *Paramicipsella*.

The original classification of Chabaud and Choquet separated the genera *Paramicipsella* and *Ornithofilaria* on the basis of the development of the cloacal papillae. However, it has been shown (1, 6) that the cloacal papillae are exceedingly variable in occurrence, size, and form in *Ornithofilaria*. Moreover,

no cloacal papillae are described on *P. stantschinskyi* (Gilbert, 1930) Chabaud and Choquet, 1953 (5). Therefore Chabaud and Choquet's basis for the separation of *Ornithofilaria* and *Paramicipsella* lacked validity. The dichotomy proposed above permits us to include species in *Ornithofilaria* which appear incongruous in *Paramicipsella*, e.g. *P. stantschinskyi*, *P. lienalis*, *P. brevispiculum*, *P. travassosi*. The following key will serve to separate the seven species which it is proposed to include in the genus *Ornithofilaria* Gönnert, including the new species *O. algonquinensis* n. sp.

Key to Species of *Ornithofilaria* Gönnert, 1937

1. Caudal papillae on male absent.....*O. stantschinskyi* (Gilbert, 1930) n. comb (5)
   Caudal papillae on male present.....2

2. Caudal papillae vestigial
   Length female 9.7–21.9 mm.; esophagus 0.95 mm. long.....
   .....*O. mavis* (Leiper, 1909) Gönnert, 1937 (9, 6)
   Length female 24–40 mm.; esophagus 0.38 mm. long...*O. fallisensis* Anderson, 1954 (1)
   Caudal papillae well developed.....3

3. Esophagus divided.....*O. lienalis* (Orloff, 1947) n. comb.[4]
   Esophagus undivided.....4

4. Esophagus very slender (approx. 6–7μ).....*O. brevispiculum* (Singh, 1949) n. comb (10)
   Esophagus broad.....5

5. Cuticular bosses present, preanal papillae 1 pr..*O. travassosi* (Koroliowa, 1926) n. comb. (8)
   Cuticular bosses absent, preanal papillae 2–3 pr.....*O. algonquinensis* n. sp.

It should be pointed out that Yorke and Maplestone, 1926 (15), designated *C. bosei* (Chandler, 1924) (3) as genotype of *Chandlerella*. *C. bosei* has been placed in the genus *Splendidofilaria* Skrjabin, 1926 (11), by Chabaud and Choquet (2). Hence the generic name *Chandlerella* is not available for use (Article 30, Ia; International Rules of Zoological Nomenclature). All the species formerly accommodated in *Chandlerella* have now been placed in other genera, e.g. *Splendidofilaria*, *Ornithofilaria*, *Paramicipsella*.

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The writer is grateful to Dr. H. B. Speakman, Director of the Ontario Research Foundation, and Dr. A. M. Fallis, Director of the Department of Parasitology, for advice and encouragement. Mr. John T. Lucker, U.S. Bureau of Animal Industry, clarified certain nomenclatorial problems associated with two of the species and the writer expressed his gratitude to him. Dr. Everett E. Wehr kindly reviewed the manuscript for which the writer is grateful. Finally I should like to express my deep appreciation to Dr. Alain Chabaud of the Institut de Parasitologie de la Faculté de Médecine de Paris for his courtesy and co-operation in this attempt to clarify the systematics of the genera discussed.

[4] *In Skrjabin and Shikhobalova 1948 (12) who give, on pages 375–6, a description of* "Chandlerella lienalis *Orloff, 1947*" *but do not list a paper by Orloff.*

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STUDIES OF THE TREMATODE *STEPHANOSTOMUM BACCATUM* (NICOLL, 1907)

III. ITS LIFE CYCLE[1]

By Robert W. Wolfgang[2]

Abstract

The life cycle of *Stephanostomum baccatum* includes an ophthalmoxiphidiocercous cercaria, lacking a penetration stylet, which develops in *Buccinum undatum* and *Neptunea decumcostatum*. The metacercaria is found in the skin and somatic muscles of pleuronectid fishes, and the adult occurs in the rectum of *Hemitripterus americanus*. A description is given of all stages.

Stafford (21) reported metacercarial cysts of *Stephanostomum hystrix* (Duj., 1845) in the fins of the winter flounder (*Pseudopleuronectes americanus* Walbaum) in Passamaquoddy Bay, New Brunswick. In 1950, the Fisheries Research Board of Canada initiated a study of the parasite to determine its possible effect on the then new and developing inshore flatfish industry, of which the winter flounder is the most important species. The work was continued during the summers of 1950, 1951, and 1952, and included a study of the distribution, incidence, and life cycle of the worm. Two papers (22, 23) dealing with the distribution and biology of the metacercaria in Canadian flatfish have been published elsewhere, while the final paper in this series will deal with the morphological variation found in adult specimens of *S. baccatum* in Canadian hosts.

The metacercaria of this species has been reported only a few times in Canada. Huntsman (3), in reviewing the biology of the American plaice (*Hippoglossoides platessoides* Fabric.)* reported small, white, subcuticular cysts in this species in the Canadian Maritimes, but did not identify them. Montreuil (personal communication) also found the cysts when working with the same species of fish in the same area in 1949.

Metacercarial cysts of *Stephanostomum species* have frequently been recorded elsewhere in the dermal and subcutaneous tissues of marine teleosts. Johnstone (4) described what is definitely a metacercaria of this genus from the fins of *Pleuronectes limanda* L. (equals *Limanda limanda*); he called it *Distomum valde inflatum* Stossich. Lebour (5) reported cysts under the skin of the dab (*Limanda limanda* L.), the long rough dab (*Hippoglossoides platessoides* Fabric.), and the witch (*Glyptocephalus cynoglossus* (L.)). Lühe (9) described metacercariae of *S. ceylonicum* in the subcutaneous tissue of *Narcine timlei* Henle. Nicoll and Small (17) reported cysts under the skin of *Limanda limanda* (L.), which they referred to as *S. baccatum*, although they produced

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Contribution from the Institute of Parasitology, McGill University, Macdonald College, P.Q., with financial assistance from the National Research Council of Canada.
[2] *Research Assistant and Assistant Professor of Parasitology.*

* *The author has examined a considerable number of American plaice from the same areas from which Huntsman and Montreuil collected their specimens, and has found numerous plaice infected with white cysts which contained the metacercaria of S. baccatum.*

no experimental proof of this identification. Nicoll (16) reported metacercariae of *S. baccatum* under the skin of *Drepanopsetta platessoides* (equals *H. platessoides* Frabic.). Yamaguti (24, 25) described cysts of both *S. japonicum* and *S. hispidum* in the skin of *Argentina kagoshimae* Jordan and Snyder, *Pseudorhombus pentophthalmus* Günther, and *Neopercis sexfasciatus* (Temme. and Schleg.). *S. hystrix* (Duj., 1845) (2), Looss, 1899, is found in the gills of *Pleuronectes platessa* (L.) and *P. maxima* (L.) (equals *Rhombus maximus* L.). Manter and Van Cleave (11) consider this species invalid although it corresponds in every way to the metacercaria of *S. baccatum* reported by Lebour, and Nicoll and Small. Yamaguti (26) refers to metacercariae which he found in *Hippocampus coronatus* Temm. and Schleg., in 1941, as *S. carangis* (*S. canagium* of Caballero, 1952).

Only one other life cycle is known for species of the genus *Stephanostomum*, namely that of *S. tenue* (Linton, 1898) which was described by Martin (12). Martin found that rediae of *S. tenue* developed in the digestive gland of the mud snail (*Nassa obsoleta* Say). The cercaria which emerged is of the ophthalmoxiphidiocercous type, is photopositive, a poor swimmer, and settles on the bottom, adhering by its tail. Martin assumed that in nature the silversides (*Menidia m. notata* (L.)) acquired the metacercarial infection by ingesting the cercaria with its food. The metacercaria occurs in the viscera of the silversides. He recovered immature adults after feeding metacercarial cysts to the puffer, *Spheroides maculatus* (Bloch and Schneider). The normal host appears to be the striped bass (*Roccus lineatus* (Bloch)).

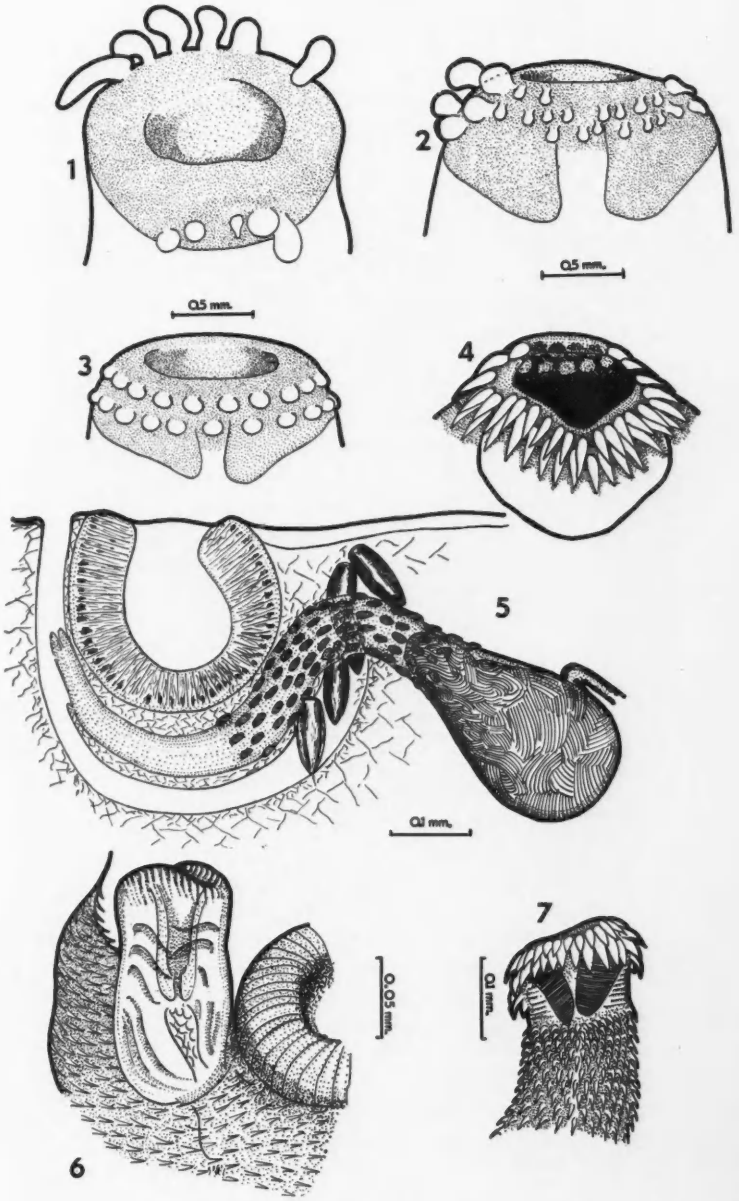
The author made all collections in the neighborhood of St. Andrews. Material from more remote localities was received through the co-operation of the following organizations: the Newfoundland Station of the Fisheries Research Board of Canada, Wood's Hole Marine Biological Station; and the U.S. Fish and Wildlife Marine Station, Boothbay Harbour, Maine, U.S.A.; Dr. B. B. Rae, Scottish Home Laboratory, Torrey, Scotland; Dr. M. Bachmansonn, Norwegian Fisheries Department. Dr. M. Hanson of the Danish Department of Fisheries supplied records of the parasite in Greenland waters. To all those who helped and to the field technicians of the Atlantic Biological Station's Groundfish Investigation, the author expresses his thanks and gratitude.

Stephanostomum baccatum (Nicoll, 1907) Manter, 1934

The Adult (*Figs. 1-11*)

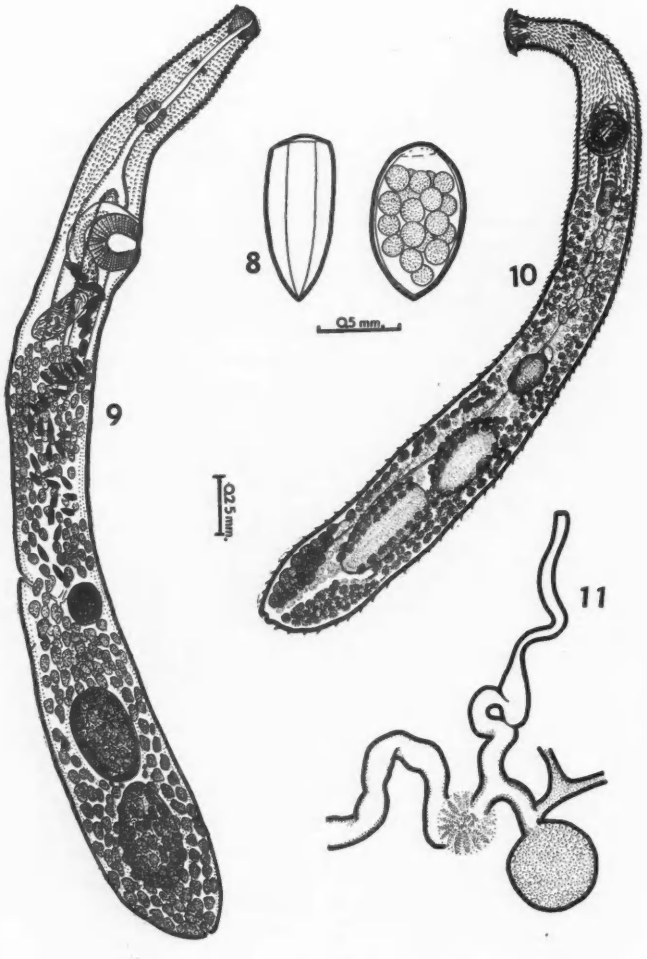
A redescription of the adult is necessary as it has been reported (as *Stephanostomum* species) only a few times: Nicoll (14), Manter (10), Miller (13). The following data are presented from an examination of approximately 1000 specimens collected from a variety of hosts.

The worms are small (1.4 to 4.50 mm. in length), thin and attenuated anteriorly and broadest (0.15 to 0.53 mm.) posteriorly at the level of the testes (Figs. 9-10). The smallest specimens were immature as judged by the



FIGS. 1-7. *Stephanostomum baccatum* (Nicoll, 1907).

FIGS. 1, 2. Irregular spination. FIG. 3. Pubescent spines. FIG. 4. Typical spines. FIG. 5. Cirrus pouch, vagina, and genital atrium. FIG. 6. Everted cirrus pouch at genital pore. FIG. 7. Lateral view of head with typical spination.



FIGS. 8-11. *Stephanostomum baccatum* (Nicoll, 1907).

FIG. 8. Eggs of *S. baccatum* (left, ribbed; right, smooth-shelled). FIG. 9. Lateral view of adult. FIG. 10. Ventral view of adult. FIG. 11. Female organs.

absence of eggs in the uterus. In cross section, the worm is oval at the posterior and round at the anterior end. The cuticle is typically covered with spines. Many specimens, however, were devoid of spines and others had spines only in the anterior part. The morphology of the spines varied from the typical form (Figs. 4, 7), broad at the insertion and pointed distally to rhomboidal and pubescent (Fig. 3). The oral sucker, which is described by Nicoll (14) as having sharp spines, had similar spination to that of the body. Grotesque and irregular spination was common (Figs. 1, 2). In specimens with typical spines, the number about the oral sucker varied from 44 to 56, the sizes of which were not uniform.

The round, terminal oral sucker (0.14 to 0.21 mm. in diameter) lies from 0.35 to 0.72 mm. from the acetabulum and has a cuticular lining which is continuous with that of the prepharynx (0.32 to 0.52 mm. in length). The prepharynx is non-muscular and was seen to telescope in living specimens when the anterior part of the worm contracted. The muscular pharynx (0.11 to 0.14 mm. in length by 0.09 to 0.14 mm. in width) is lined with cuticle and varies from pyriform to barrel-shaped. There is a very short esophagus which cannot be seen in contracted specimens. It is histologically continuous with the caeca and divides into two posteriorly-directed caeca just anterior to the acetabulum. The lumen of the caeca are compact and small near the acetabulum but increase to about twice their anterior breadth near the posterior end. They terminate at the posterior end of the worm. There is no uroproct.

The strongly muscular acetabulum (0.12 to 0.27 mm. in diameter) lies about the middle of small worms but may occur in the anterior fifth in elongate ones. It is from completely round to oval in shape and in some specimens protrudes ventrally, decreasing its diameter and forming a distinct salience. The ratio of the acetabulum to the oral sucker is from 1 : 1 to 1 : 9.

The short genital sinus reaches to about the middle of the medial edge of the acetabulum. The cirrus pouch (0.18 to 0.56 mm. long) is claviform and sinuous and follows the medial contour of the acetabulum (Fig. 5). In some specimens, however, it continues in a straight line from the genital sinus to just below the dorsal surface. The cirrus is unarmed (Fig. 6). In the posterior fourth of the cirrus pouch is a sacculate seminal vesicle (0.10 to 0.23 mm. long). Prostatic glands lie along the wall of the cirrus pouch anterior to the seminal vesicle. The musculature is similar to that described for *S. casum* (Linton, 1910) by Pratt (20). The metraterm is unarmed and not muscular; its histology is similar to that of the uterus. The thin-walled uterus is sinuous in short specimens but straight to loosely folded in long ones. The eggs were seen to be pushed anteriorly and out of the genital sinus by pressure of the parenchyma as a result of peristalsis of the body in live specimens.

The gonads lie in the posterior part of the body with the ovary generally contiguous with the two testes. The ovary may be located from the middle to beginning of the posterior fourth of the body length in the mid-ventral

plane. A short oviduct extends anteriorly from the ovary and is joined dorsally by Laurer's canal which opens on the dorsal surface (Fig. 11). In immature adults and well developed metacercariae the oviduct broadens into the uterus at a point surrounded by the massed cells of the Mehlis gland. In fully developed adults these cells become dispersed in the parenchyma. There is no true seminal receptacle; the lower portion of the uterus serves this function.

The tandem testes lie posterior to the ovary, separated from it by the union of the lateral excretory ducts at the beginning of the excretory vesicle. In the larger worms the posterior testis is generally the larger, but in smaller ones and well-developed metacercariae, they are about the same size (approximately twice the size of the ovary).

Some specimens have dense vitelline follicle development while in others it is light and diffuse. The follicles may extend posteriorly from just anterior to the posterior edge of the acetabulum to slightly posterior to the cirrus pouch. The greatest concentration of vitellaria is about the caeca although in specimens showing many follicles they may extend to the medial area around all organs. They invade the spaces between the testes and ovary if these are not contiguous and fill the post-testicular space. Follicles are not confluent across the ventral surface but may be across the dorsal surface.

The excretory vesicle is tubular and dorsal to the testes. It bifurcates posterior to the ovary giving rise to two lateral, anteriorly directed excretory tubules which extend to the level of the oral sucker.

Location: Lower intestine and rectum.

Hosts: In Canada: Sea raven (*Hemitripterus americanus*),
Arctic eelpout (*Lycodes* sp.),
Wrymouth (*Cryptocanthodes maculatus*),
Halibut (*Hippoglossus hippoglossus*), and the
Short-horned sculpin (*Myoxocephalus scorpius*).

In arctic and European waters:
The father lasher (*Cottus scorpius*) and the halibut.

Experimental hosts infected which were not found naturally infected were the long-horned sculpin (*Myoxocephalus octodecimspinosus*) and the ocean pout (*Macrozoarces americanus*).

Distribution: Across the North Atlantic Ocean from Maine in the United States to the Bay of Fundy, Nova Scotia, and Newfoundland in Canada. The Davis Strait in Greenland, and the North Sea in Europe.

Discussion

S. baccatum was first described by Nicoll (14) from the halibut (*Hippoglossus hippoglossus* L.) in British waters; he (15) later described six specimens from the father lasher (*Cottus scorpius* L.). Manter (10) records it from the halibut

in Maine waters. Manter and Van Cleave (11) give the following footnote (on p. 327) on this species: "Nicoll's original specimen of *S. baccatum* had vitellaria extending only to the base of the cirrus sac. He later described a somewhat more anterior extent but not to the acetabulum. Manter's (10) figure shows the vitellaria to the acetabulum. Thus there is some uncertainty regarding this character in this species."

Stafford (21) recorded *S. sobrinum* (Levinsen, 1881) Looss, 1901, from the sea raven (*Hemitripterus americanus* Gmelin), the arctic eelpout (*Lycodes* sp.), and the wrymouth (*Cryptocanthodes maculatus* Storer) in Canadian waters. In reviewing Stafford's collection Miller (13) considered these specimens to be *Stephanostomum* sp. inq., as he could not determine the number of spines.

Stafford's identification of the specimens recovered from Canadian hosts as *S. sobrinum* has been queried by Caballero (1), who considers them to be *S. tenue* (Linton, 1898) Martin, 1938, because the distribution of *S. tenue* is contiguous with that of the specimens reported by Stafford, and because *S. tenue* has been recorded by Linton (8) from the sea raven near Wood's Hole. The writer has examined Stafford's specimens and finds them to be *S. baccatum*. He has also examined Linton's specimens (which were loaned through the courtesy of Dr. E. W. Price, U.S. National Museum) and has found them to differ from his own specimens of *S. baccatum* from the sea raven in Canada.

S. baccatum extends southward to the known northern limit of *S. tenue* and it is possible that the distribution of the two species may overlap. The author has, however, examined in Canada numerous recorded hosts of *S. tenue* without finding any specimens of this species.

Levinsen (7) inadequately described *S. sobrinum* from *Cottus scorpius* in Greenland waters, and Odhner (19) reported but did not redescribe it from the same host in unspecified arctic waters. Although Levinsen's description of *S. sobrinum* is vague it agrees essentially with that of *S. baccatum*. In view of the hosts and the distribution of the parasite, *S. sobrinum* and *S. baccatum* are probably conspecific. Neither Levinsen's nor Odhner's specimens were available to the present author.

As the type specimens of *S. baccatum* are no longer available, and are believed to have been lost with Nicoll's effects in the Pacific, it is proposed to redescribe the species and to discuss its validity and that of related species.

The Egg

There are two types of eggs (75 to 90 μ): ovoid, smooth shelled, slightly flattened at the opercular end, and an elongate ribbed form (Fig. 8). The hexagonally ribbed eggs were described by Manter (10) from his specimens of *S. baccatum* from the halibut in Maine. He considered them characteristic of the genus, but a number of species have been described since that time with smooth shells, by him and other authors. As both types of eggs occur in the same specimens of the author's collections, he does not consider one or the other as being specific to this species. The ribbed eggs appear to be infertile

as they are transparent (containing no staining cells) and undergo no development in the laboratory. They are slightly thinner than the smooth-shelled type. The smooth-shelled eggs do undergo development but none produced recognizable miracidia; in mounted specimens the enclosed cells take the stain. Ribbed eggs are most common in spring and summer collections while the smooth-shelled forms predominate in the winter. The miracidium was not studied.

The Rediae (*Figs. 12-14*)

Two types of rediae were recovered from snails (Fig. 12): immature and mature. The immature rediae (0.5 to 1.5 mm. in length) are blunt at the stomal and pointed at the aboral end. The simple stoma is followed by a muscular pharynx and a gut (Fig. 13) which occupies most of the remaining space in the body cavity. There are a number of germ cells at the posterior end of the body which were considerably smaller than those in the gravid rediae.

The mature or gravid rediae are larger (3.0 to 4.0 mm. in length) and are irregular in shape (Fig. 14). They contain 6 to 16 cercariae, usually in different stages of development. The cercariae move about in response to light and, as no birth pore is present, are liberated by rupture of the redia cuticle. Remnants of germ cells and cercariae frequently are released simultaneously. Both the immature and mature rediae are capable of movement outside the host.

The color of the rediae ranges from white to yellow, the yellow being derived from the host tissue on which the organism feeds.

Location: Gonads and digestive gland.

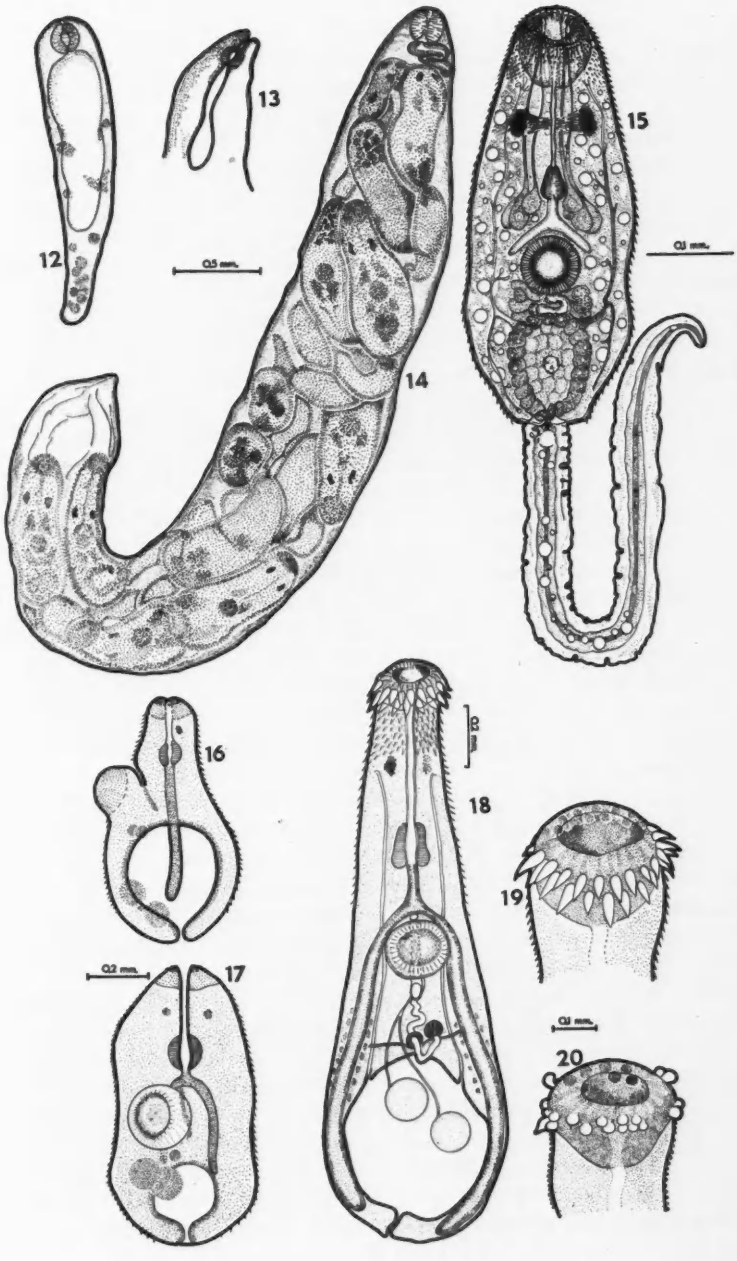
Distribution: Specimens of infected snails were collected from: Passamaquoddy Bay, Bay of Fundy (Grand Manan), and Annapolis Basin, N.S.

Hosts: Common whelk (*Buccinum undatum*),
Ten-banded whelk (*Neptunea decemcostatum*).

Discussion

Infections, with one exception, were always heavy and there was destruction of most of the gonadal and digestive gland tissue. Castration, due to the presence of asexual stages of trematodes, which has been reported by other investigators for other species, almost certainly occurs in this case also. The massive size of the infections suggests that the infection builds up over a

FIGS. 12-20. *Stephanostomum baccatum* (Nicoll, 1907).
FIG. 12. Immature redia. FIG. 13. Stomum, pharynx, and gut of mature redia. FIG. 14. Gravid redia containing cercariae. FIG. 15. Cercaria. FIGS. 16, 17. Young metacercariae. FIG. 18. Well-developed metacercaria. FIG. 19. Oral spines of metacercaria (typical). FIG. 20. Oral spines of metcercaria (irregular and pubescent).


12
13
0.5 mm.
14
15
0.1 mm.
16
18
0.2 mm.
19
0.2 mm.
17
0.2 mm.
20

period of time and that the release of cercariae is simultaneous. No cercariae were found emerging naturally from infected snails. Infected gastropods were detected only by dissection. The rediae recovered from massive infections were all gravid, cercaria-producing forms. In the lightly infected snail immature rediae were recovered together with larger rediae which contained organisms more closely resembling rediae than cercariae. It seems probable that where such heavy infections occur, a series of rediae-producing generations is necessary.

The rediae of *S. baccatum* resemble those described by Martin (12) for *S. tenue* and there were no morphological characteristics of this stage which the author could find useful in aiding the determination of its species.

The Cercaria (*Fig. 15*)

The cercariae liberated by dissection from infected snails were in various stages of development. The fully developed cercariae were capable of violent, sporadic movement in sea water. They move tail first—the tail whipping in the form of a figure eight. No cercaria was seen to rise more than a few millimeters from the bottom of a vessel filled with sea-water. Once settled, the cercariae crawl on the bottom and then become quiescent and remain so unless subjected to strong light when they thrash their tails violently and contort their bodies. Light does stimulate the cercariae to move violently although they make no effort to enter it when the light is placed adjacent to their location. Movement, then, could not be determined as directed but rather as random wandering. The cercariae frequently adhered to the glass by the tip of the tail as do cercariae of *S. tenue*. The tail is detached easily and the cercariae may continue wandering by means of the oral sucker and acetabulum for some time afterward. The maximum life of the cercariae in sea-water held at 16° to 18° C. was three days.

The cercaria (0.32 to 0.50 mm. in length by 0.09 to 0.14 mm. in width—living specimen) is of the ophthalmoxiphidiocercous type which has secondarily lost its penetration stylet. In no specimen, regardless of the state of development, was a stylet seen. The shape is variable depending on the state of contraction. There are two unicellular penetration glands, lying on either side of the postpharyngeal region. The two eyespots are located about midway between the oral sucker and the pharynx, one on either side of the prepharynx. In living specimens they could be seen to be connected by a fibrous commissure. The pharynx is typically pyriform and muscular, preceded anteriorly by the prepharynx and followed by a short but distinct esophagus which branches in front of the acetabulum to form two short caeca. These never reached posterior to the posterior edge of the acetabulum. The oral sucker (0.06 to 0.08 mm. in diameter) is terminal. The acetabulum (0.05 to 0.07 mm. in diameter) is weakly muscular in comparison to the oral sucker, and is located about the middle of the body. The genital primordia lie posterior to the acetabulum and are followed by the large, globular, and heavy-walled excretory vesicle. Two lateral tubules communicate with the anterior

end to the vesicle which passes through a postmedian opening into the tail excretory duct. The tail is variable in shape (0.54 to 0.64 mm. long in relaxed specimens), muscular, and capable of strong peristalsis. The excretory duct terminates in a pore at its tip.

Spines, if present, are poorly developed. Cuticular armament varied in morphology in specimens from the same host, some well-developed cercariae being devoid of spines. Stomal spines, as described by Martin (12) for *S. tenue* were not observed.

Discussion

An attempt was made to study the flame cell pattern which has proved useful in determining the species of larval trematodes in general. Owing to the large number of lipoid-like vacuoles within the bodies of both the cercariae and the rediae, the body is opaque even in specimens newly extracted from the gonad of the snail. In the cercaria a few cells were seen near the oral sucker and near the posterior end of the body which were in groups of two or three, but no complete pattern could be made out, although a large number of specimens was examined.

When placed in dishes containing flounders, the cercariae made no attempt to attack the fish. If, however, they were placed on the flounder or came in contact with it accidentally, they immediately attached themselves to it by their tails or oral sucker and began an augur-like motion which seemed to assist penetration. Only those cercariae which managed to work their way under scales or to attach near skin devoid of scales (near the fin membrane or on it) succeeded in penetrating. The time required for penetration seemed to vary with the density of the dermal tissue at the point of attachment and smaller fish were always more easily penetrated than large ones (23).

In nature, the ventral surface of the flounder is more heavily infected than the dorsal. Winter flounders and their relatives are peculiar in that they bury themselves in bottom debris when resting, by tossing bits of bottom material over their backs. The flopping motion associated with this habit causes the scales to collect under them small bits of sand or mud. The cercaria settles on the debris after emerging from its host and it would appear that it is this fortuitous association which gives it access to the skin of the flounder. The presence of the metacercaria in the gills of some bottom-dwelling fish is explained by their habit of grovelling for food (e.g. the sea raven), and thus picking up in their gill rackers bits of cercariae-laden debris.

Cercariae for infection experiments were recovered by dissection of whelks. Infected snails were always easy to determine by the gray appearance of their gonads caused by the large number of asexual stages in this organ. When the mantle membrane of an infected animal is observed under the dissection microscope it has a peppery appearance that is due to the large number of eyespots of the contained cercariae.

When the rediae rupture, the cercariae are released into the gonads of the snail and occur free there together with the rediae. Cercariae were found

alive in all stages of development, liberated into the gland tissue, and it would seem that underdeveloped forms can complete their development there, after liberation from the redia.

The cercaria of *S. baccatum* is distinctly different from that of *S. tenue*. It resembles most closely *Cercaria neptunae* of Lebour (6). Both are alike in morphology and dimensions; the hosts are similar (*Buccinum undatum* for both, *Neptunea antiqua* for *C. neptunae*, and *N. decemcostatum* for *S. baccatum*), and Lebour reported that she was unable to find a penetration stylet in any of her specimens. She considered her cercaria to be the larval form of *Acanthopsolus lageniformis* Lebour, 1910 (synonym of *Neophasis pusilla* Stafford, 1904) although she carried out no experiments to prove this relationship.

The Metacercaria (*Figs. 16-20*)

Table I gives the comparative sizes of both newly encysted and older metacercaria.

TABLE I

MORPHOLOGICAL COMPARISON OF METACERCARIAE OF *Stephanostomum baccatum*

	Newly encysted	Well-developed
Length	0.44 – 0.56 mm.	1.50 – 2.40 mm.
Width	0.23 – 0.25 mm.	0.55 – 0.66 mm.
Oral sucker	0.09 – 0.11 mm.	0.135 – 0.222 mm.
Sucker ratio	1 : 1	1 : 1
Prepharynx	0.04 mm.	0.41 mm.
Pharynx	0.04 × 0.04 mm.	0.09 × 0.135 mm.
Caeca	Short (solid)	Long to posterior end, lumenate
Oral spines	Very small (not countable)	35–36
Excretory vesicle	Heavy-walled, small primordial cells	Thin-walled, voluminous, developed, small testes dorsal to excretory vesicle, in wall
Spination	Variable in shape, when present, poorly developed	Variable in shape, when present, well developed

Cysts vary in size from that of the cercaria (0.4 mm.) from 1.0 to 1.8 mm. in diameter. Cysts lying in the myotomes assume the ovoid shape, conforming to the longitudinal axis of the myotome as the connective tissue is laid down in this direction. The envelopment of the newly-formed cyst by connective tissue is noted by the comparative difficulty with which the cyst is removed. The cyst adheres to its site and is quite elastic. Upon dissection, older cysts pop out of the encystment site leaving behind an adventitious pocket.

The metacercaria of *S. baccatum* is always located in peripheral tissues. Specimens have been collected from the gills of both normal and facultative hosts but because the cysts are found frequently in dermal and subcutaneous tissues the gill infestation is considered atypical.

When the cercaria reaches the encystment site it secretes a hyaline membrane around itself and, in the presence of a strong light, may be seen to move within the membrane. When encystment is completed, there is a white, opaque concretion in the excretory vesicle which is not seen in the cercaria. Examination of this material suggests that it is lipoid in character; it dissolves in lipid solvents and stains with Sudan III. No further analysis of the material was made. A white adventitious cyst of host origin develops around the parasite membrane in due course. The laying down of collagenous fibers begins soon after the parasite is *in situ* and continues throughout the life of the fish. The formation of a dense adventitious outer cyst is characteristic of cutaneous and subcutaneous cysts but not necessarily of those in the gills. Regardless of the location of the cyst there were seldom any pigment granules.

The newly encysted metacercaria is similar in morphology to the cercaria, the main difference being the large concretion in the excretory vesicle (Figs. 16-17). It has very short caeca, poorly developed suckers of about equal size, postacetabular cell aggregates which represent genital primordia and large, dark prepharyngeal eye spots. The metacercaria becomes motile when subjected to strong light. Spination is variable in structure and oral spines are too small to be counted.

The fully-developed metacercaria is adult-like in morphology (Fig. 18) and may be from two to twelve years of age. This estimate is based on the age of its host, the flounder, which may be infected during its first year (23). The suckers are well developed and about equal in size; the prepharynx, pharynx, and caeca are well developed. The cirrus pouch is elongated and contains a small seminal vesicle at its posterior end. The uterus is developed and originates in a compact Mehlis gland which lies anterior to a small but distinct ovary. The testes are small and globular and resemble those of the adult. The excretory vesicle is large and filled with a white concretion. The walls of the excretory vessel are thin and the excretory pore is sealed off by a membrane which breaks easily if pressure is applied, liberating the excretory material into the cyst. In some of the older specimens vitelline primordia were observed and the common yolk ducts and Laurer's canal are visible. In larger specimens, the eye spots are much reduced in comparison to the size of those of the newly encysted metacercaria. The advanced metacercaria is lethargic when exposed to strong light.

Location: Gills, dermal tissues, and somatic muscles.

Hosts: *In North America:*
Winter flounder (*Pseudopleuronectes americanus* Walbaum),
Smooth flounder (*Liopsetta putnami* (Gill)),
Brill (*Lophopsetta aquosa* (Mitchill)),
Yellow tail (*Limanda ferruginea* (Storer)),
Witch (*Glyptocephalus cynoglossus* (L.)), and the
American plaice (*Hippoglossoides platessoides* (Fabric.)).

In European waters:
Witch,
Long rough dab (same as American plaice),
Dab (*Limanda limanda* (L.)),
Lemon sole (*Microstomus kitt* (Walbaum)), and the
Plaice (*Pleuronectes platessa* (L.)).

Distribution: Similar to that of the adult.

Discussion

The author has frequently found cysts in the gills of bottom-dwelling teleostal fish, other than pleuronectids. The most important of these is the sea raven which acts also as the natural definitive host. This suggests an intimate association between the gastropod intermediate host and the final host, which would facilitate the perpetuation of the trematode. Nicoll (17) has reported cysts of *Stephanostomum baccatum* in the adventitious tissue of the intestine of the angler (*Lophius piscatorius* L.) in the North Sea. It is probably another species and not *S. baccatum*. Although the author has examined a number of these fish he has failed to find them infected in the western Atlantic.

Control of the experiments was insufficient to permit of a study the growth of the metacercaria (23). Examination of metacercariae from fish caught over a three-year period has, however, led the author to surmise that development is slow. This hypothesis is supported by the fact that observation showed that a year was required for gonadal development and that the metacercaria appeared to continue its development beyond that time.

S. hystrix (Duj., 1845) Looss, 1899, was described by Dujardin (2) from cysts occurring in the gills and in the mouth of heterosomatic fishes in Europe, as follows: ". . . (non-adulte.) Corps blanc, long de 1 mm, 6 à 2 mm, large de 0 mm, 5, de forme très-variable et souvent lágeniforme ou cylindrique, obtus en arrière, et prolongé en avant par une sorte de cou épineux, que termine la tête globuleuse, large de 0 mm, 2, entourée d'un double rang d'épines plus longues; — ventouse ventrale large de 0 mm, 18, située au milieu de la longueur; — bulbe oesophagien très grand, large de 0 mm, 16 situé à la base du cou en avant de la ventouse ventrale et séparé de la tête par un tube etroit et long; — intestin bifurqué immédiatement en arrière de la ventouse ventrale, et envoyant ses branches jusqu'à l'extrémité postérieure; — oriface postérieur donnant entrée dans une vaste cavité ventrale remplie d'une substance blanche opaque; — deux vaisseaux latéraux sinueux dans toute la longueur de corps."

Caballero (1) is in error in his reference to *S. hystrix*, in misinterpreting the decimal point in the total length. He states (p. 124): "Según F. Dujardin, la descripción fué hecha sobre ejemplares de larvas enquistadas cuyo cuerpo es blanquecino, de 1 mm. a 6.2 mm. de largo . . ."

Manter and Van Cleave (11) consider *S. hystrix* invalid because they consider it has been insufficiently described.

Although the adult was not described and although the number and size of the spines are not given, Dujardin's description of the metacercaria agrees with descriptions given by other European authors and by the present author (23) for the metacercaria of *S. baccatum*. The reference only to gill and oral infections for *S. hystrix* is insignificant because although the metacercariae of *S. baccatum* commonly infect the skin and subcutaneous tissues, gill infections are very common.

The life cycle of *S. baccatum* differs from that of *S. tenue* in several important respects. The metacercaria of the former species occurs in the muscles, gills, and subcutaneous tissues of flat-fishes (facultatively in the gills of other bottom-dwelling teleosts). *S. tenue*, on the other hand, encysts in the viscera of its intermediate host. The differences in the cercariae are not great, although the presence of a penetration stylet in *S. tenue* and the lack of one in *S. baccatum*—a dermal penetrator with presumably a more difficult association of tissues to be encountered on the route to its encystment site—is surprising.

In no case was *S. baccatum* found to produce extensive pigmentation in association with its cysts, even in flatfish like the brill, which are extremely sensitive to dermal irritation. The other major dermal cyst-producing species in Passamaquoddy Bay, *Cryptocotyle lingua* Creplin (a heterophyid) almost always causes the production of pigmentation in association with its cysts. Nigrelli (18) found some cysts of *C. lingua* in the ocean pout which were not pigmented and concluded that pigmentation of trematode cysts is primarily a matter of location and that those larvae which encyst in areas of a low density of pigment-producing cells acquire the least degree of pigmentation. In flounders, the ventral surface is peculiarly devoid of pigmentation. In flounders infected with *S. baccatum* cysts and with *C. lingua* cysts on the same surfaces, cysts of the latter species were pigmented while those of the former were not. This seems to indicate that an irritant is present in *C. lingua* and absent from *S. baccatum*. It is possible that *S. baccatum* has been a parasite of flounders for a long time and has become adapted to life in the tissues of this fish.

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STUDIES OF THE TREMATODE *STEPHANOSTOMUM BACCATUM* (NICOLL, 1907)

IV. THE VARIATION OF THE ADULT MORPHOLOGY AND THE TAXONOMY OF THE GENUS[1]

By Robert W. Wolfgang[2]

Abstract

The morphological variation of the adult of *Stephanostomum baccatum* is described and taxonomic criteria of the genus *Stephanostomum* are discussed.

Introduction

In 1899 Looss (11) created the genus *Stephanostomum* for five trematodes previously included in the pseudogenus *Distomum* Rez. In 1901 (12) he changed the name *Stephanostomum* to *Stephanochasmus* because Daniellson and Koren, in 1880, had used the name *Stephanostoma* for another group of animals. Thereafter, both names are found in the literature and, in 1934, Yamaguti (22) introduced the name *Echinostephanus* for certain Japanese-Pacific species of the genus. In 1938 Ward (19) considered *Echinostephanus* to be synonymous with *Stephanochasmus*. In 1940 Manter (15) pointed out that Looss' original name (*Stephanostomum*) was valid according to Article 36 of the International Rules of Zoological Nomenclature, and he proceeded to make new combinations of existing species which were assigned to genera other than *Stephanostomum*. Dawes (6, 7), Hanson (8), Manter and Van Cleave (17), and Caballero (3), have followed Manter's example. In addition, Manter and Van Cleave and Caballero constructed keys for the separation of species of this genus.

All species occur as adults and metacercariae in marine teleost fishes, and the rediae and cercariae develop in marine gastropods. The genus has a world-wide distribution although most species occur in hosts in tropical waters.

The separation of the species of *Stephanostomum* is still a matter of considerable difficulty, in spite of the keys prepared by Manter and Van Cleave (17) and by Caballero (3). The criteria which have been used for this purpose include body form, sucker ratio, degree of muscular development of the metraterm, size of cirrus, and especially, the number and shape of the oral spines and the vitellarian pattern.

Materials and Methods

In order to determine the extent and variation of the vitellaria and the variation in other morphological structures of *S. baccatum*, a study was made of 100 specimens (Table I), which represented part of a single infection

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(totalling some 400 specimens) from the rectum of a single sea raven. All the specimens were collected, relaxed, and prepared for study *en masse*, no conscious effort being made to apply cover glass pressure to the specimens in mounting them. It is the author's experience that worms which are fixed and processed by the usual dehydration procedure are not subject to great distortion of somatic relationships. On the other hand, worms freshly collected and compressed previous to fixing may be greatly altered from their natural form. Ulmer (18) has discussed in detail the effects of compression of trematodes prior to fixing.

In Table I, the data from these specimens are grouped according to length classes. It will be noted that the length-range of the first group is greater than that for subsequent groups, because more large than small specimens are available in this collection.

Specimens were relaxed prior to fixation in Bouin's fluid and were stained in Mayer's paracarmine. Specimens were not compressed during either fixing or mounting.

Results

A study of this table shows that variation in proportional parts of the body is greater in smaller than in larger specimens; for example, the measurement from the anterior end to the acetabulum varied from 0.31 to 0.63 mm. in the smallest length class, while in the 2.71 to 2.80 mm. class, it varied only from 0.81 to 0.91 mm. in length. There are similar variations for other body measurements. The prepharynx increases in length with increased body length but may vary as much as twice its minimum length even in the largest class of worm. In many of the smallest worms studied, the pharynx had attained its maximum size and its length seems to be reliable as an aid to classification; its shape, however, is variable. In most specimens, the caeca were obscured by the vitelline follicles. The oral suckers varied from 0.12 to 0.18 mm. in diameter, and the acetabulum from 0.14 to 0.24 mm. in the smallest size class, while the oral sucker varied from 0.18 to 0.20 mm. and the acetabulum from 0.23 to 0.27 mm. in diameter in worms of 2.80 mm. or over in length. The sucker ratios were from 1 : 1 to 1 : 8 for the specimens studied in this series. Although with increased size of worm there is a corresponding increase in size of the suckers, the range of the sucker ratios does not change materially: each class is essentially comparable to the next. Sucker form and shape are variable.

The gonads show no reliable degree of constancy; the relationship in size of the ovary to the testes is roughly 1 : 2. The gonads are usually contiguous, although some exceptions were seen in attenuated worms. The distance separating the ovary from the anterior testis is never over 0.19 mm.

In this species the metraterm and cirrus are unarmed. The genital sinus is short and relatively constant in length; it is unarmed. It is difficult to measure the cirrus pouch accurately except in specimens mounted on their sides; in most specimens it is sinuous, accommodating itself to the medial

TABLE I

Stephanostomum baccatum (NICOLL, 1907) COLLECTED FROM THE SEA RAVEN BASED ON 100 MEASURED SPECIMENS*

Length class	1.17–1.70	1.71–1.80	1.91–2.00	2.01–2.10	2.11–2.20	2.21–2.30	2.31–2.40	2.41–2.50	2.51–2.60	2.61–2.70	2.71–2.80	2.81 plus
Width	0.26–0.36	0.22–0.34	0.28–0.41	0.28–0.45	0.23–0.43	0.26–0.44	0.31–0.36	0.28–0.39	0.27–0.41	0.33–0.45	0.28–0.40	0.32–0.36
Oral sucker	0.12–0.18	0.13–0.15	0.13–0.17	0.14–0.20	0.14–0.18	0.13–0.18	0.14–0.18	0.14–0.16	0.14–0.19	0.14–0.19	0.17–0.18	0.18–0.20
Acetabulum	0.14–0.24	0.14–0.26	0.19–0.23	0.18–0.25	0.18–0.23	0.18–0.24	0.19–0.23	0.18–0.25	0.18–0.25	0.20–0.27	0.21–0.23	0.23–0.27
Cirrus pouch	0.27–0.28	0.23–0.48	0.38–0.50	0.36–0.50	0.36–0.50	0.34–0.45	0.32–.050	0.37–0.50	0.39–0.50	0.36–0.50	0.41–0.54	0.41–0.52
Seminal vesicle	0.10	0.07–.016	0.11–0.18	0.14–0.18	0.14–0.18	0.10–0.20	0.14–0.19	0.14–0.18	0.14–0.18	0.18–0.23	0.18–	0.16–0.20
Pharynx	0.07–0.14 × 0.09–0.14	0.08–0.14 × 0.13–0.14	0.09–0.14 × 0.13–0.16	0.09–0.11 × 0.13–0.18	0.09–0.14 × 0.14–0.06	0.08–0.17 × 0.13–0.37	0.10–0.14 × 0.10–0.14	0.10–0.14 × 0.11–0.14	0.10–0.14 × 0.11–0.18	0.09–0.14 × 0.10–0.21	0.10–0.14 × 0.13–0.14	0.14 × 0.14–0.16
Prepharynx	0.18–0.29	0.20–0.34	0.25–0.38	0.20–0.36	0.27–0.36	0.27–0.51	0.27–0.38	0.32–0.42	0.27–0.36	0.24–0.41	0.32–0.45	0.32–0.45
Ovary	0.05–0.10	0.06–0.09	0.08–0.12	0.08–0.15	0.09–0.14	0.09–0.12	0.09–0.14	0.07–0.14	0.09–0.14	0.06–0.14	0.11–0.14	0.11–0.14
Testis, anterior	0.09–0.18	0.11–0.30	0.14–0.23	0.16–0.24	0.10–0.22	0.17–0.23	0.16–0.27	0.21–0.23	0.14–0.27	0.13–0.27	0.23–0.36	0.20–0.25
Testis, posterior	0.09–0.18	0.13–0.23	0.18–0.25	0.19–0.27	0.18–0.23	0.18–0.27	0.18–0.27	0.22–0.32	0.16–0.27	0.14–0.32	0.27–0.32	0.23–0.24
No. of ova	4–10 (0)	6–11 (0)	2–19	4–22	1–19	3–17	8–15	11–26	12–26	6–32	15–24	16–23
Acetabulum–anterior	0.31–0.63	0.41–0.65	0.56–0.72	0.54–0.69	0.54–0.76	0.54–0.72	0.68–0.77	0.50–0.81	0.63–0.81	0.63–0.86	0.81–0.91	0.90
Acetabulum–vitellaria	*0.00–0.13*	*0.00–0.12*	*0.03–0.14*	*0.00–0.19*	*0.00–0.14*	*0.00–0.23*	*0.01–0.23*	*0.07–0.20*	*0.05–0.18*	*0.00–0.18*	*0.00–0.14*	*0.05–0.24*
Ovary-acetabulum	0.18–0.37	0.36–0.50	0.41–0.50	0.41–0.69	0.45–0.54	0.41–0.63	0.54–0.63	0.50–0.90	0.47–0.72	0.36–0.77	0.51–0.72	0.66–0.81
Ovary–testis	0.00–0.14	0.05–0.17	0.00–0.07	0.05–0.11	0.04–0.11	0.07–0.17	0.08–0.23	0.09–0.11	0.09–0.18	0.06–0.74	0.08–0.19	0.13–0.18
Post-testicular space	0.09–0.31	0.09–0.26	0.11–0.18	0.11–0.22	0.18–0.25	0.09–0.25	0.14–0.23	0.17–0.26	0.18–0.30	0.15–0.31	0.15–0.27	0.26–0.31
Sucker ratio	1 : 1.2–1 : 1.6	1 : 1.1–1 : 1.4	1 : 1.2–1 : 1.8	1 : 1.1–1 : 1.6	1 : 1.1–1 : 1.6	1 : 1.1–1 : 1.8	1 : 1.1–1 : 1.5	1 : 1.1–1 : 1.8	1 : 1–1 : 1.6	1 : 1.2–1 : 1.4	1 : 1.2–1 : 1.5	1 : 1.2–1 : 1.5
No. of worms	7	9	10	9	10	13	8	10	9	8	5	2

* *All measurements in mm.*

curve of the acetabulum. The cirrus pouch is 0.27 to 0.28 mm. long in the smallest specimens but almost reaches its maximum length of 0.23 to 0.48 mm. in the second group (1.71 to 1.80 mm. in length); its greatest length is 0.54 mm. The distance the cirrus extends posterior to the acetabulum is relatively constant.

Although the anterior limit of the vitellaria was variable from specimen to specimen, the variation was relatively constant for each length class. In terms of morphological relationship, the anterior border of the vitellaria varies in position from just in front of the posterior edge of the acetabulum to slightly behind the posterior end of the cirrus pouch. The extent of development is also variable. Some specimens have sparse vitelline follicle development: others show a dense follicular growth. The invasion of spaces separating the gonads was observed only in attenuated specimens having the maximum vitelline follicle development. In others, the follicles were limited to the caecal areas and were interrupted ventrally opposite the gonads and uterus.

Variation of the vitellaria appears to be related in part to the age of the metacercaria when entering the definitive host. Some excysted and attached adolescent worms recovered from the rectum of the sea raven had vitellaria more poorly developed than those of the most highly developed metacercariae recovered from the flesh of winter flounders, in which the rudiments of the vitelline follicles were already present. The crowding effect of the vitellaria in some of the worms collected during the study of the life cycle might be due to glandular development proceeding more rapidly than somatic growth. The vitellaria in species of this genus, with the exception of those showing interruptions opposite the gonads, seem to occupy all the available body space posterior to their anterior origin. This does not explain the fact that many specimens of *S. baccatum* show a very poor vitelline development. Unfortunately, as it was impossible to study the development of the vitellaria experimentally it is also impossible to come to any conclusions regarding such development.

If sufficient material is available to make *en face* preparations, the spines can be counted easily. Unfortunately, one must conclude from a study of the literature that such material has not been available.

Spination in *S. baccatum* seems to be related to the degree of thickness of the cuticle which appears to be a congenital condition. Where the cuticle is dense and thick, spines are generally well developed; where it is thin, spines are either poorly developed or lacking. This condition occurs also in the metacercariae and the cercariae. In individuals with a well-developed spination, the spines drop off during growth as the posterior cuticle becomes thinner because the cuticular matrix in which these spines are embedded becomes a poor anchorage. In general, in specimens freshly collected from the gut, the spines withstand considerable rough treatment without becoming detached. Manter's (16) suggestion that abnormal spination (i.e. grotesque spination) may be the result of regeneration following injury is not supported

by the work of Beaver (1) who, studying the regenerative capacity of Echinostomes, found that most wounds heal and undergo some regeneration of structure, but that spines, once removed, are not replaced in any form. It can, therefore, be assumed that such abnormalities as do appear are the result of the peculiar growth characteristics of the individual. From an examination of collections of both well- and poorly-spined *S. baccatum* from the same host (sea ravens) in the same area, the author concludes that no importance can be attached to spination as a taxonomic criterion in *S. baccatum*. Most of the European material which he examined showed well-developed spines as did most of the material collected from offshore flounders in Canadian waters; this appears to be the normal type. On the other hand, inshore collection of specimens from Passamaquoddy Bay, New Brunswick, and St. Mary's Bay, Nova Scotia, showed a wide variety of spination; these were the areas with the highest incidence of the parasite (20).

The cause of this wide variation in spine structure in inshore forms is unknown. It would appear from the data available on incidence in Canada (20, 21) that these two bays provide optimum conditions for survival and perpetuation of the parasite. It is a matter for conjecture whether the ease with which the parasite may complete its life cycle in Passamaquoddy Bay has led to the production of species undergoing mutation, or whether it allows the easy survival of forms less well equipped to survive elsewhere.

The excretory bladder is seldom seen with sufficient clarity to be of much use in determining the identity of species.

The eggs are variable in size and number, and egg production (maturation) begins before the worms are fully grown.

Useful Criteria for Identifying Species

Considered together, certain morphological characters may be of diagnostic value in defining the species of *Stephanostomum*. The cirrus pouch and the morphology of the cirrus, the morphology of the metraterm or vagina, the sucker ratio, the size of the pharynx—but not its shape—the length of the genital atrium, the length of the post-testicular space, and the structure of the Mehlis gland (whether compact or diffuse), all show a sufficient degree of constancy to warrant consideration in evaluating the validity of species. The vitellarian pattern is variable and is of value only in so far as it shows interruptions opposite the testes. The presence or absence of a uroproct is valuable in helping to identify species.

The terminal genitalia, although not characteristic for genera of this family, appear to be characteristic for the species of this genus; however, this character has not been used uniformly in classification. The cirrus and the vagina or metraterm show similar morphological characteristics peculiar to each species. If the cirrus is armed, the metraterm is strongly muscular and similarly armed: if the cirrus is unarmed, the metraterm is non-muscular or poorly supplied with muscles and unarmed.

The similarity in the structural characteristics of the vagina and the cirrus suggests that they are developed from a common precursor. The structure of these organs may be sufficient to warrant the erection of two subgenera (18 species with armed and 12 with unarmed genitalia). Armament has usually been described as small spines or scales on the cirrus and within the metraterm, but Manter (16) described *S. promocropsi* and *S. coryphaenae* as having tubercles.

In *S. baccatum*, the sucker ratio is variable, but the limitations are such that the acetabulum is never smaller than the oral sucker, and never reaches twice the size of that organ. Some species show more marked inequalities in sucker ratios, e.g. *S. fistulariae* (1.4–1.7 : 1) and *S. microstephanum* (1.2–4.6 : 1) have oral suckers which may be less than half the size of the acetabulum.

In most species the length of the pharynx is about 0.14 to 0.26 mm. but in *S. imparispine* it is 0.45 mm., in *S. hispidum* 0.35 mm., in *S. casum* 0.40 mm., in *S. tenue* 0.32 mm., and in *S. promicropsi* 0.25 to 0.36 mm. long. On the other hand, *S. pristis* and *S. caducum* each have a pharynx measuring only 0.10 mm. in length. The shape of the pharynx, in contrast to its size, is of little value in classification because of its extreme variability.

The length of the genital atrium is perhaps one of the most important single morphological characters of use in classification. Manter (14) has suggested that some species seem to differ so markedly in this character as to make it doubtful whether they are *Stephanostomum* species. *S. tenue*, *S. cesticillum*, *S. hispidum*, *S. cloacum*, *S. bicoronatum*, *S. pristis*, *S. caducum*, and *S. lineatum* all have long genital atria. Other species have short genital atria.

The length of the post-testicular space is of doubtful value in classification and is included here only because it accents the differences existing between some species. In species with vitellaria interrupted lateral to the gonads, the space is long as in *S. caducum*, *S. pristis*, and *S. lineatum*. In others, it may be long or short, but in *S. baccatum* it is short in specimens of medium size (about 2.0 mm. long) but longer in specimens measuring up to 4.50 mm.

In discussing the general disposition of species of this genus, the Mehlis gland cannot be used as a criterion as it has been insufficiently described in most species. In *S. casum*, *S. baccatum* and many other species, it is diffuse: in *S. bicoronatum* (the cotypes of which the writer has had the opportunity of examining through the courtesy of Mr. M. Prudhoe, British Museum (Natural History), it is compact. Several authors have described the Mehlis gland as occurring dorsally and slightly anterior to the ovary. As most specimens are mounted ventrally it is, therefore, difficult to study this gland without sectioning. In *S. bicoronatum*, it lies directly dorsal to the ovary and is visible as a distinct and separate cellular mass which is joined to Laurer's canal and the uterus by accessory tubules. (This structure has not been referred to in the tables presented later in this paper.) In the metacercariae which have been described for *Stephanostomum* species, the Mehlis gland usually appears as a compact mass beside the ovary; in some, but evidently not in all species it becomes diffuse as the worm matures.

A uroproct has been reported for some species but not for others. However, as it is difficult to see even when present, it may have been missed in some species. It is lacking in *S. baccatum*.

Host distribution, which has been used by some authors as a criterion in separating species, does not seem to be valid, nor does geographical distribution of the parasite or its hosts when one considers the extremely wide range of some species (e.g. *S. dentatum*, *S. casum*, and *S. ditrematis*). *S. baccatum* and *S. tenue* both occur in the sea raven but apparently in contiguous rather than the same localities.

According to Dawes (6), the British species of *Stephanostomum* are not well established but he lists five species from British hosts:

S. pristis (Deslong in Lamouroux, 1824),

S. caducum (Looss, 1901),

S. rhombispinosum (Lebour, 1908) (which Caballero synonymizes with *S. pristis*),

S. triglae (Lebour, 1908), and

S. baccatum (Nicoll, 1907).

Unfortunately, the specimens of these species are not at present available. However, if one disregards oral spination as a taxonomic criterion, the differences separating *S. caducum* and *S. pristis* disappear, and spination (number and size) is the main difference separating *S. triglae* and *S. baccatum*. Were the species in question reduced to synonymy there would appear to be only two valid species in British waters: *S. baccatum* and *S. pristis*. If Caballero's (3) designation of *S. lebourae* stands there would be a third, although this species awaits confirmation by an examination of the actual specimens.

Species of the Genus *Stephanostomum*

Using as criteria for showing species affinities and differences, the pattern of the vitellaria (whether interrupted lateral to the gonads or not), cirrus armed or unarmed, long or short, the writer has placed into five groups (Table II) the species considered valid in the latest publication (Caballero (3)).

From Table II, Group 1, it will be seen that *S. baccatum* shows no valid differences from *S. triglae*. *S. japonicum* and *S. californicum* differ from each other only in the anterior extent of their vitellaria and pharynx size. *S. fistulariae* and *S. elongatum* differ mainly in sucker ratio, although the length of the post-testicular space and the size of the pharynx in *S. fistulariae* may be important characters. *S. tenue* differs from all the others in having a long genital atrium and a large pharynx. The similarity of *S. sobrium* with *S. baccatum* has already been discussed.

Group 2 shows that *S. cesticillum*, the type species, is distinct from all other species in this group in having a long genital atrium and long post-testicular space. *S. microstephanum* can be separated easily by its unusually large oral sucker. *S. casum* is distinguished by its large pharynx, which is

TABLE II

MORPHOLOGICAL AFFINITIES OF SPECIES OF *Stephanostomum*

Species	Genital atrium	Sucker ratio	Egg size	Post-testicular space	Uroproct	Pharynx	Condition of the cirrus
Group 1. Vitellaria uninterrupted, cirrus short and unarmed							
S. baccatum (Nicoll, 1907) Manter, 1934	Short	1 : 1–18*	75–91μ	Short	Absent	0.20–0.21 × 0.12–0.16	
S. triglae (Lebour, 1908) Dawes, 1946	Short	1 : 1–1	99μ	Short	?	0.20	
S. japonicum (Yamaguti, 1934) Manter & Van Cleave, 1951	Short	1 : 1.7–2.0	100–130μ	Short	Absent	0.15–0.19	
S. californicum Manter & Van Cleave, 1951	Short	1 : 1.5	99μ	Short	Absent	0.29	
S. fistulariae (Yamaguti, 1940) Manter & Van Cleave, 1951	Short	1 : 4–1.7 : 1	60–70μ	Long	Present	0.20–0.28	
S. elongatum (Park, 1939) Hanson, 1950	Short	1 : 1.3	60–70μ	Short	Present	0.16–0.17	
*S. tenue*** (Linton, 1898) Martin, 1938	Long	1 : 1.6	60–80μ	Short	Absent	0.32	
Group 2. Vitellaria uninterrupted, cirrus short and armed							
S. minutum (Looss, 1901) Manter, 1940	Short	1 : 1.2–1.8*	50–80μ	Short	?	0.11–0.25	
S. cesticillum (Molin, 1858) Looss, 1899	Long	1 : 1.2	80μ	Long	?	Small ?	

S. dentatum (Linton, 1901) Linton, 1940	Short	1 : 1.3–1.4	70μ	Short	Absent	0.15–0.16
S. casum (Linton, 1910) McFarlane, 1934	Short	1 : 1.4–1.7	80μ	Short	Present	0.40
S. megacephalum Manter, 1940	Short	1 : 1–1.1	60–70μ	Short	Present	0.18–0.26
S. microstephanum Manter, 1934	Short	1.2–4.6 : 1	60–70μ	Short	Absent	0.15–0.17
S. coryphaenae Manter, 1947	Short	1 : 1.4–1.5	70–80μ	Short	Absent	0.18–0.19
S. carangium (Yamaguti, 1951) Caballero, 1952	Short	1 : 1.4	60–70μ	Short	Present	0.15–0.18
S. tristephanum McFarlane, 1936	Short	1 : 1	78–84μ	Short	?	0.78 in diameter; no length given
Group 3. Vitellaria uninterrupted, cirrus long and unarmed						
S. imparaspine (Linton, 1905) Manter, 1940	Short	1 : 1.2*	70μ	Short	?	0.45
S. hispidum (Yamaguti, 1934) Manter, 1940	Long	1 : 1.6	70–80μ	Short	Present	0.35
S. cloacum (Srivastava, 1938) Manter & Van Cleave, 1951	Long	1 : 1–1.5	60–70μ	Short	Present	0.25

* *Measurements in millimeters unless otherwise indicated.*
** *S. sobrinum (Lev. 1881) Looss, 1899, probably fits into this group but is omitted because the description is incomplete.*

TABLE II—*Concluded*

MORPHOLOGICAL AFFINITIES OF SPECIES OF *Stephanostomum*—*Concluded*

Species	Genital atrium	Sucker ratio	Egg size	Post-testicular space	Uroproct	Pharynx	Condition of the cirrus
Group 4. Vitellaria uninterrupted, cirrus long and armed							
S. bicoronatum (Stoss., 1883) Manter, 1940	Long	1 : 1.9–2.4*	60–80μ	Long	Present	0.24	
S. anisotremi Manter, 1940	Short	1 : 2.0–2.6	60–70μ	Short	Absent	0.26–0.37	
S. lebourae Caballero, 1952	Short	1 : 1	80μ	Short	Absent	Small (?)	
S. ditrematis (Yamaguti, 1939) Manter, 1947	Short	1 : 1.2–1.5	60–70μ	Short	Present	0.11–0.30	
S. multispinosum Manter, 1940	Short	1 : 1.3–1.4	70–80μ	Short	Present	0.20	
S. robustum (MacCallum, 1917) Caballero, 1952	Short	1 : 1.1	70μ	Short	Absent	0.18	
Group 5. Vitellaria interrupted lateral to the gonads							
S. pristis (Deslong., 1824) Looss, 1899	Long	1 : 1.2*	60–80μ	Long	?	0.10	Armed and long
S. caducum (Looss, 1901) Manter, 1934	Long	1 : 1	60–70μ	Long	?	0.10	Armed
S. lineatum Manter, 1934	Long	1 : 1.5–1.6	60–70μ	Long	Absent	Small ?	Armed and long
S. promicropsi Manter, 1947	Short	1 : 1.7–1.8	50–60μ	Short	Absent	0.25–0.36	Unarmed and Short

* *Measurements in millimeters unless otherwise indicated.*

approximately twice the size of that organ in other species of the group. It has not been shown whether *S. minutum* has a uroproct and so its relationship to *S. dentatum* and *S. carangium* is not clear. *S. carangium* and *S. dentatum* differ in that the latter has a uroproct and the former has none. *S. tristephanum* is similar to *S. megacephalum*, differing from it mainly in having a very short prepharynx and larger eggs. It differs from *S. microstephanum* in having a very different sucker ratio.

Group 3 shows that *S. hispidum* and *S. cloacum* are very similar; they differ mainly in the number of oral spines and distribution of the vitellaria. The host distribution of both species is contiguous. *S. imparaspine*, although similar to the other two species in the group, has a short genital atrium and a very large pharynx. In this group, however pharynx size may be relatively unimportant as this organ is large in all three species.

Group 4 shows that *S. ditrematis* and *S. multispinosum* differ on the basis of the total length of the worm and the structure and arrangement of the gonads. *S. ditrematis* has wide distribution in both the Atlantic and Pacific, while *S. multispinosum* occurs only in the Pacific. *S. bicoronatum* differs from all other species in having a long genital atrium. *S. anistotremi* and *S. lebourae* are similar but the description of the latter species is based on a description of *S. caducum* by Lebour (9), and the species are from different geographical areas. Manter (15) considered *S. robustum* similar to *S. sentum* (which he made a synonym with *S. minutum*) but the length of the cirrus seems to distinguish it from this species. Caballero's (3) reference to its similarity to *S. hispidum* is understandable, except that *S. hispidum* has an armed cirrus. *S. robustum* differs from *S. anistotremi* in having a smaller pharynx and considerably different sucker ratio.

The first three species in group five appear to be very closely related. *S. pristis* and *S. caducum* have constantly been reported from the same locality and from similar hosts. *S. lineatum* has been reported from gadid hosts in other localities and it differs from *S. caducum* and *S. pristis* mainly in the size of the suckers and number of oral spines. Caballero (3) points out the similarity of this species to *S. pristis* and *S. rhombispinosum* (synonym of *S. caducum* according to Caballero). *S. promicorpsi* differs distinctly from other species in the group in having a short genital atrium, a short post-testicular space, a much larger pharynx, and a short unarmed cirrus.

The data presented in Table II are taken from original descriptions of the species and from Caballero's (3) monograph. As not all species have been described equally well, it is probable that some characters when studied more extensively will show differences from the original descriptions. The continuous emphasis on spination and vitellarian extent has undoubtedly caused some slighting of other characters which this study has shown to be important. The author is of the opinion that no attempt to construct keys or other aids to classification can be successful until a greater number of species is thoroughly examined.

Related Genera*

The variations noted in the oral spines of *S. baccatum* have some bearing upon the status of two other genera in the family Acanthocolpidae Lühe, 1909. This family originally contained three genera, namely: *Stephanostomum* Looss, 1899, *Acanthocolpus* Lühe, 1906, and *Deropristis* Odhner, 1902. Detailed discussions of the progressive changes in the family have been given by Ward (19), Cable and Hunninen (5), and recently, by Caballero (3) and Cable (4). The latest revision (that of Caballero (3)), includes two subfamilies: Acanthocolpinae Lühe, 1906 and Pleorchinae Caballero, 1952. The latter contains the single genus *Pleorchis* Railliet, 1896: Cable and Hunninen (5) have suggested that this genus deserves no more than generic status. The Acanthocolpinae includes nine genera the relationship of which to the family depends primarily upon the genital organs, the arrangement of the gonads, and the fact that a prepharynx is always present and a seminal receptacle always lacking. The three genera, *Neophasis* Stafford, 1904 (syn. *Acanthopsolus*), *Lepidauchen* Nicoll, 1913, and *Pseudolepidepidon* Yamaguti, 1938, have been placed at some time in the family Allocreadiidae. Cable and Hunninen (5) and Caballero (3) place them in the Acanthocolpidae, Dawes (7) in the Allocreadiidae. Until their status is clarified, the author is of the opinion that they should remain in the Acanthocolpidae.

The genus *Tormopsolus* Poche, 1926, was erected for *Distomum osculatum* Looss (12). Looss was uncertain as to the position of this species believing it might be a *Stephanostomum* which had lost its oral spines. Manter (14) queried the validity of the genus, as did Dawes (7), who believes that the two genera might be synonymous. He cites the few specimens which have been reported and the few species described. Hanson (8) has recently accepted the genus as valid, in extending the distribution of *T. orientalis* Yamaguti, 1934, to Bermuda, and Caballero (3) has created *T. lintoni* for a species from Wood's Hole, Mass. There are three species in the genus which are similar to *Stephanostomum* species except that they lack oral spines. The writer has examined a number of specimens of *Stephanostomum* which lacked oral spines, but provided the worms were otherwise well clothed in body spines, has been able to demonstrate scars where spines had been. Spination in *S. baccatum* is related to cuticle density and where body spines are lacking, oral spines are also lacking; the various degrees of development seen in oral spines is reflected in a similar development in body spines. Following the suggestions of Ward (19), who proposed criteria on which to base generic and specific classification, the writer is in doubt as to the validity of spination as a criterion in separating genera of the family, especially as it contains several genera without this character, such as *Lepidauchen*, *Pseudolepidepidon*, *Neophasis*, *Pleorchis*, and

* *Yamaguti (23) separates the Acanthocolpidae from other related families by the following criteria: "Cirrus and metraterm spined, ductus hermaphroditicus present." As approximately half of the species are not described as having armed genitalia, this character in Yamaguti's key is confusing. He includes a number of other genera: Skrjabinopsolus Ivanov, 1935, Pristicola Cable, 1952, and Pristotrema Cable, 1952, in his listing and places Pleorchis in a separate family Pleorchiidae.*

Acanthocolpus, the type genus. When the sole criterion for genus distinction is a character which has been shown to be variable within the family, it is probable that *Tormopsolus* must eventually be considered a synonym of its closest relative, *Stephanostomum*.

The genus *Dihemistephanus* Looss, 1901, was created for *Distomum lydae* Stoss., 1896, from the intestine of the sun fish. Little (10) created *D. sturionis* from the royal sturgeon, and gave a new generic description. As Cable (4) states, Little's description is based primarily on the characters of *D. sturionis* rather than on the type species from which it differs. Cable has removed the questionable species to another family, which leaves the genus with one species. Looss, in creating *D. lydae*, stated that it was very similar to *Stephanostomum* differing only in the arrangement and type of oral spines. Cable's able discussion demonstates clearly the uncertainty with which the genus is veiled. Caballero (2) has recently created a new genus, *Manteria*, for the only other species, *D. brachydera*. Yamaguti (23) considers it a subgenus of *Dihemistephanus*. The confusion surrounding the position of recent species of the genus, which all have been removed to other genera, indicates the unsatisfactory condition of the generic diagnosis. The writer believes that unless a further investigation of the type species reveals a greater number of distinguishing characteristics, this genus should also become a synonym of *Stephanostomum*.

Despite the exhaustive work of Caballero (3) in revising the family, its status and that of several of its genera remain unsatisfactory. Ward's (19) proposed criteria for revisions seem to be the most reasonable to date. Ward felt that the family is most closely related to the Echinostomatidae. Dawes (6, 7), on the other hand, believes it to be closely related to the Allocreadiidae. Cable (4) has suggested that, on the basis of life-cycle studies, it resembles neither. The writer agrees with Cable, although the superficial resemblance of most of the adults to those of the Allocreadiidae and families related to it, is more pronounced than to any other suprageneric group. As this family is more extensively studied the situation will improve, but at present the writer agrees with Dawes' (6, p. 214) opinion that: "in view of pending changes we must be satisfied with an array of genera."

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A PROVISIONAL LIFE TABLE FOR THE BARREN GROUND CARIBOU[1]

By A. W. F. Banfield

Abstract

A provisional life table for the continental Barren Ground caribou, *Rangifer arcticus arcticus* (Richardson), has been prepared from a collection of 292 mandibles collected in 1948 and 1949 on the summer and winter ranges of the species in northern Canada. The data include both sexes. The age of the specimens was estimated by the eruption and wear of the teeth. The mean expected life span at birth was found to be 4.09 years. The average mortality rate for the first 10 years of life was 71%. The apparent potential natural longevity was about 13 years.

Introduction

Life tables of natural populations have been prepared for few species of mammals. Deevey (4) indicated a method of preparing such a table using Murie's (6) data for the white sheep, *Ovis dalli dalli*. Bourliere (2) prepared a life table for the chamois, *Rupicapra rupicapra*, based upon Couturier's (3) data. Recently Kurten (5) has produced life tables for a number of fossil mammal populations.

During a preliminary investigation of the Barren Ground caribou, sponsored by the Canadian Wildlife Service, Department of Northern Affairs and National Resources, a collection of mandibles was made to provide a basis for a preliminary life table for the species.

Collection of Specimens

Three hundred and two single mandibular rami were collected from carcasses found in northern Manitoba and Saskatchewan and in Mackenzie and Keewatin Districts of the Northwest Territories. The causes of death varied. The majority were ascribed to hunters. Other factors were: wolf predation, accidental deaths (drowning), and disease. A number were from specimens collected for examination during the investigation (Banfield (1)).

Determination of Age

Unfortunately the antlers of caribou do not provide a means for easily determining age as do the horns of sheep and chamois. It was first necessary to devise a method of determining the age of the specimens found. Following the work of Severinghaus (7) measurements were made on the lingual side of the tooth row from gum line to crest. In addition, the wear on each tooth; the wear on the posterior cusp of the third molar; and the relative widths of enamel and dentine on the first molar, were recorded (Banfield (1)).

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Contribution from the Canadian Wildlife Service Department of Northern Affairs and National Resources, Ottawa, Ontario.

The approximate age at death was known for a series of 35 specimens up to the age of three years. These were mandibles taken from specimens collected and hunters' kills examined. The age was determined by date and location of the kill, measurements, weight, sexual maturity, and antler development. Since the caribou is a migratory species and collections were made on summer and winter ranges, it was often possible to assign approximate ages to many other specimens of young caribou—either in the whole or half-year class depending upon location of the carcass.

It was found possible to determine the age of caribou up to three years with fair accuracy based upon the eruption of the deciduous and permanent teeth as little wear occurred prior to that date.

A further check was provided by comparison with a series of 12 reindeer *(Rangifer arcticus asiaticus)* mandibles from tagged animals of known age, from six months to eight and one half years. These came from the Departmental reindeer herd near the mouth of the Mackenzie River. It was found that the eruption and wear of the teeth of reindeer up to three years of age approximated that of the teeth of the caribou series of estimated similar age.

The remainder of the series of caribou mandibles were segregated into classes based upon the progressive wear of molars and premolars.

The approximate age of these class intervals was estimated by comparison with a graph of tooth wear of reindeer of known age.

It was found necessary to discard 10 mandibular rami because actinomycotic lesions had caused loss of teeth and uneven wear. This condition made accurate determination of age impossible for these specimens. The sample, therefore, consisted of 292 specimens. The age classification of the specimens is presented in Table I.

TABLE I

APPROXIMATE AGE DISTRIBUTION OF THE 292 CARIBOU MANDIBLES

Approximate age in years	Number of mandibles found
0–1	44
1–2	51
2–3	60
3–4	22
4–5	23
5–6	12
6–7	15
7–8	17
8–9	13
9–10	12
10–11	13
11–12	6
12+	4

Findings

A provisional life table for both sexes of the Barren Ground caribou is presented in Table II. This table follows the conventional form and headings

TABLE II

PROVISIONAL LIFE TABLE FOR THE BARREN GROUND CARIBOU *(Rangifer arcticus arcticus)* BASED ON THE ESTIMATED AGE AT DEATH OF 292 CARIBOU SKULLS FOUND ON THE OPEN RANGE

x	x'	d_x	l_x	$1000\,q_x$	e_x
Age in years	Deviation of age classes as percentage of mean age	Number dying in age interval out of 1000 born	Number surviving at start of age interval from 1000 born	Mortality rate per 1000 alive at start of age interval	Expectation of life: mean life time remaining to those attaining age interval
0–1	−100	151	1000	151	4.09
1–2	− 76	175	849	206	3.7
2–3	− 51	202	674	300	3.6
3–4	− 27	75	468	160	3.9
4–5	− 2	79	393	201	3.6
5–6	22	41	314	131	3.4
6–7	46	51	273	187	2.8
7–8	71	58	222	261	2.3
8–9	95	45	164	275	2.0
9–10	120	41	119	345	1.5
10–11	144	45	78	577	1.1
11–12	169	20	33	607	0.9
12+	193	13	13	1000	0.5

as described by Deevey (4). The age intervals x into which the sample was divided are given in the first column. These age intervals are indicated as percentage deviations from the mean life expectancy x' in column two. (This column provides a way of comparing the survival curve with those of other species.) The number of deaths d_x in the age interval, from an initial cohort of 1000 born, is given in column three. The number of survivors from the cohort l_x is shown in column four. The mortality rate q_x on a per 1000 basis is given in column five. The expectation of life e_x is given in column six. It is derived from the formulae:

$$\text{Age structure, } L_x = \tfrac{1}{2}\,(l_x + l_x + 1)$$

$$e_x = T_x/l_x$$

Successive values of L_x are summed from the bottom of the column up to each age group x. This gives T_x the total number of animals × age units still to be lived by animals of age x. Expectation of life is obtained by dividing T_x by l_x.

The survivorship curve is presented in Fig. 1. The survival axis has been graduated on a logarithmic scale. In this way mortality rates are reflected in the slope of the curve regardless of the strength of the cohort. It will be noted that up to the age 10 years the curve is of the rectangular type, indicating a constant mortality rate. After that period it becomes convex and resembles the curve for *Ovis dalli dalli*. The slope of the curve is reported to indicate the average mortality according to Kurten (5). A fitted curve for the first section of the curve up to the 10th year has an indicated average mortality rate of 71%. This is similar to rates calculated for a number of species by Kurten.

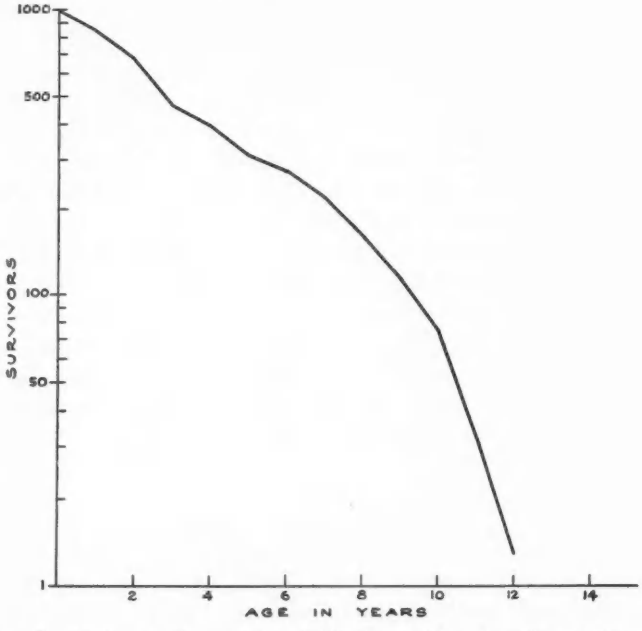

FIG. 1. Survival curve for a series of 292 Barren Ground caribou. The survival curve is graduated on a logarithmic scale.

Discussion

Ecological data on mammal populations seldom provide a census by ages of those alive and deaths by ages for a single population. It is therefore seldom possible to present a dynamic life table. In this case a time-specific life table has been constructed from a sample of the population of Barren Ground caribou. This table characterizes the caribou population sampled during 1948 and 1949.

In order to accept the table it is necessary to make certain assumptions. Firstly, that the sample was random and represented the population of caribou at the time. Secondly, that the population was stable in time so that actual

age distribution and life table distribution are identical. It is evident from a description of the material that these assumptions are only approximately true. The sample may have been biased somewhat by the wide use of native hunters' kills. The natural roles of predation and disease were difficult to assess. In addition, field studies (Banfield (1)) have indicated that the annual increment of calves varied from year to year. There was no indication however that the total population changed significantly during the investigation.

Some bias was introduced into Murie's sheep data by the perishability of the lamb skulls and the underrepresentation of this age class in the sample. In the case of the caribou there seems to be a preponderance of the younger classes due in part to selective hunting patterns of the natives, for calf and yearling hides are sought for garments.

The present life table has been considered provisional because of the experimental errors involved in the collection and identification of the material. It is granted that there is a variation in tooth wear with age which would introduce errors in the determination of age of the specimens.

Several factors have led me to conclude that the data are relatively valid. In the first case, the specimens came from such a wide range in northern Canada that any geographical variation in wear would be nullified. Secondly, a number of graphs were prepared by grouping age classes as high as three year intervals. This process would lessen the effects of errors in accurate age determination. In each case the survivorship curve maintained its basic form.

It was thought to be of interest, therefore, because later surveys could produce comparable data which would reflect the success of management practices such as control of predation, hunting, and range conditions.

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AGGRESSIVE BEHAVIOR OF UNDERYEARLING KAMLOOPS TROUT[1]

By G. E. Stringer[2] and W. S. Hoar[3]

Abstract

The aggressive behavior of juvenile Kamloops trout (*Salmo gairdneri kamloops* Jordan) consists of chasing, nipping, retreating, threatening, and fighting. These different components are described. Territorial defence appears to be the end result of this behavior. Aggressiveness disappears at low light intensity when the fish settle to the bottom and remain quiet. A seasonal decline in aggressive behavior seems to occur during the spring. The sign stimulus releasing attack is a moving fish-shaped object approximately the same size as the trout. Dark colors have a stronger releasing value than bright colors. Fins and color patterns do not seem to be involved in the sign stimulus.

Introduction

Breder (2) has discussed the relationship between aggressive and schooling behavior of fish and pointed out that schooling fish show little or no aggressive behavior while a "peck-order" is marked in non-schooling forms. The Salmonidae show interesting differences in this respect with representatives such as pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) which school compactly while others such as coho salmon (*O. kisutch*) and rainbow trout (*Salmo gairdneri*) occupy and defend territory and show varying degrees of aggressive behavior. Coho salmon show changes in the intensity of aggressive behavior at the time of the smolt transformation and in strongly schooling species, aggressive behavior sometimes appears as a displacement reaction (7).

Although aggressive behavior of salmon and trout has doubtless been observed frequently and although a general description of this behavior in *Oncorhynchus* has been given (5, 7), no detailed analysis in juvenile salmonids seems to have been made. In this paper the aggressive behavior of juvenile kamloops trout (*Salmo gairdneri kamloops* Jordan) is described and an attempt made to identify the releaser mechanism. The term "trout" when used in this paper refers to the underyearling fish which had hatched in mid-June.

Materials and Methods

Experiments and observations were carried out at the University of British Columbia from 1951–1954 during the months October to April. Trout were reared at the Cultus Lake Trout Hatchery, Sardis, B.C.. Sizes of fish are given in connection with the various experiments.

Trout were observed in glass aquaria 180 cm. long, 18 cm. wide, and 25 cm. deep—inside dimensions. Inlet and outlet portions were screened and the

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actual length of aquarium available to the fish was 140 cm. Water flowed in at one end and out the opposite through an overflow pipe which maintained a depth of 10 cm. The flow, approximately 670 ml. per min., was sufficient to create a slight positive rheotaxis but insufficient to stimulate fish to swim into the current. One or more fish often "faced" the outlet end for long periods. Thus, the artificial conditions of the aquarium would simulate conditions in a pool rather than a stream in so far as velocity of flow is concerned.

Six fish were used in each aquarium and observed for two days. They were not fed during this period. Lights were turned on in the morning and four to six hours allowed for adaptation before observations were begun. Light intensity at the water surface varied from 10.5 ft-c. at either end to 12 ft-c. at center of the tank.

Results

Chasing, nipping, threatening, fighting, and defence of specific territories are regularly observed in a group of trout maintained under these conditions. These varied activities are collectively referred to as "aggressive behavior". The terminology is based on a rather subjective interpretation of what is happening. It is difficult, however, to find other terms which categorize the behavior patterns in a more descriptive manner.

Nipping is the action most frequently observed. It has been described in juvenile coho salmon where ". . . one fish makes a quick darting movement toward, and bites usually close to the base of another fish's tail. The action does not involve any contact between fish for only the water near the attacked fish is "bitten"." (5). Nipping behavior differs in trout since actual contact is frequent and any part of the fish may be bitten. It varies from mere chasing without biting to attacks which may displace the recipient one or more inches sideways. The action seems to be more frequently directed toward the caudal region of the attacked fish but this may be due to the rapid retreat of the latter (Fig. 1, A). Aggressiveness is not a continuous activity like schooling but varies markedly between different groups and even in the same group from time to time. Figs. 2–4 indicate the degree of variability which may be expected.

Chasing and nipping are the predominant but not the only components of the aggressive behavior of trout. Activities referred to as *threatening*, *fighting*, and *territorial defence* are associated with nipping. On one occasion, during eight hours of observation 534 nips were associated with 43 definite threats and 19 retaliations. Although this ratio varies, the predominant role of nipping is always evident.

The threatening act of trout, like the char (4), involves an erection of fins, especially the dorsal and pectorals, and frequently a twisting of the caudal portion of the body until it makes a sharp angle with the anterior part (Fig. 1, B). The angular position may vary 90° from horizontal with head either up or down. Swimming is jerky with sideward torsion of body accentuated.

FIG. 1. A, nipping behavior; B, threatening behavior; C, fighting behavior or retaliation.

Increased body undulations may compensate for the retarding effect exerted on forward motion by the extended fins. Positions of threatening fish are similar to those depicted for stickleback (10, 12) and char (4). In the stickleback, however, the head is always pointed downwards (12). An additional display in brown trout and juvenile char (4) is the simultaneous erection of the branchiostegal membrane and a lowering of the hyal bones. This phenomenon has not been noted in kamloops trout. Tail blows and water jets characteristic of some fighting fish (10) were not observed.

Threatening is often a prelude to what is termed fighting. In fighting, two fish swim around in a close circle repeatedly attacking each other (Fig. 1, C). This behavior closely parallels fighting among spawning kamloops trout and char (4). Threatening is intense when the fish are fighting. The actual behavior varies with the response of the attacked fish. The initial movement of the attacking fish is followed by chasing and nipping if the attacked fish flees, while threatening and frequent fighting occurs if the attacked fish does not flee. The chain of reactions seems to depend on the intensity of the fight drive of the attacked fish. When the intensity of the drive is high, the attacked fish will threaten and frequently retaliate vigorously but when the drive is low, flight takes place. This behavior of trout closely parallels the fighting behavior of sticklebacks (12), except that trout display no activity comparable to spine fighting.

Threatening, chasing, and fighting are associated with territorial behavior. Defence of specific territories seems to be the only evident result of these varied activities. Trout, like many other animals, remain for long periods within specific, circumscribed areas and usually move from these only to feed or to attack intruding fish. One or two fish in an experimental group are often actively aggressive. They are termed "dominants", the others are termed "subordinates". Occasionally a fish may change from dominant to subordinate in a very short time. However, a temporarily subordinate fish will usually re-establish a territory previously held. In the groups observed, one or two were usually dominant for long periods; some became aggressive and held territories for shorter periods, while the remainder (one or four) rarely nipped and did not defend areas or become dominant.

A well organized peck-order is recognized in the aggressive activities of hens (1) and some fish (8). No such order was evident in general observations on trout. However, certain fish did dominate and in an attempt to establish precise organization within the group, fish were marked distinctively and a record made of their individual activities. Five different groups each of six fish were observed for a total of 21 hr. These trout ranged in size from 5.4 cm. to 7.2 cm. Temperature varied from 12.8° C. to 15.6° C. during the course of the experiment. Data for four of the groups are summarized in Table I. The number I fish nipped all others with about equal intensity. A few exceptions are evident. Observations indicated that in these cases the relatively larger number of nips was elicited by the relatively greater swimming activity of the nipped fish. The number VI fish did little or no nipping. In intermediate position fish were nipped about as often as they nipped. This type of order is typical of the behavior of pigeons. Allee (1) states: "In the long run one becomes fairly sure which bird in each of the groups will dominate in the larger number of contacts, but the result of the next meeting between two individuals is not to be known with certainty until it has taken place. Within the same hour and even within a few minutes reversals in dominance may take place. . . ." This same phenomenon is true of trout.

Effect of Light Intensity

A series of five lights (60 w. each) were suspended above the aquarium and rheostats placed in the circuit so that light intensity could be readily altered from 0 to 15 ft-c. at water surface. Changing the light intensity did not noticeably startle the trout.

In studying the effect of decreasing illumination, light was reduced from maximum (15 ft-c.) to 12 ft-c. and after five minutes, a 10 min. record of nipping was started. This procedure was followed with five minutes' adaptation and 10 min. observation for the series 12, 8, 6, 4, 2.5, 1.5, 0.75, and 0.25 ft-c. In additional experiments, light intensities were increased in increments of 0.5 ft-c. from 0 to 4 ft-c. Observations were for 15 min. at each intensity. Lights had been turned off four to six hours prior to starting these observations.

TABLE I

NUMBER OF NIPS BY EACH OF SIX FISH DIRECTED TOWARD OTHER MEMBERS OF THE GROUP. ROMAN NUMBERS, THE ATTACKING FISH; MARGINAL ARABIC NUMBERS, THE FISH ATTACKED; AGGRESSIVENESS OF FISH ARRANGED IN DESCENDING ORDER

Fish attacked	Attacking fish						Attacking fish					
	I	II	III	IV	V	VI	I	II	III	IV	V	VI
1	—	22	15	3	6	4	—	12	4	6	0	0
2	81	—	12	20	14	4	30	—	19	7	3	0
3	116	12	—	15	1	0	54	67	—	16	2	1
4	218	14	27	—	25	4	47	6	21	—	4	0
5	104	52	21	8	—	11	83	17	19	48	—	0
6	104	17	13	11	7	—	25	45	39	24	4	—
Total	623	117	88	57	53	23	239	147	102	101	13	1
1	—	33	13	0	2	0	—	60	14	51	14	5
2	47	—	19	29	31	12	80	—	54	35	37	1
3	74	48	—	21	21	2	126	73	—	46	67	4
4	85	63	64	—	12	7	60	42	31	—	23	9
5	175	85	18	16	—	19	79	43	105	30	—	4
6	79	45	18	15	14	—	79	53	55	65	49	—
Total	460	274	132	81	80	40	424	271	259	227	190	23

Effect of light as a limiting factor on aggressiveness is shown in Fig. 2. No general decline is evident until illumination is reduced to 4 ft-c. Below this intensity the decline is rapid but rises promptly again with increasing illumination. Elsewhere (unpublished data) it has been shown that this decline in aggressiveness with decreasing light is associated with settling of underyearling coho to the bottom. Observations indicate the same phenomenon is true of trout.

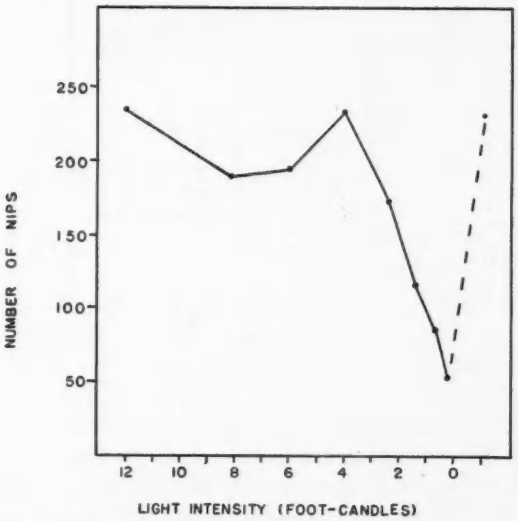

FIG. 2. Effect of decreasing illumination on total number of nips recorded in eight series of observations; three groups each with six fish; total observation time, 36 hr.; temperature range, 8.1° C. to 11° C.; fork lengths of fish, 58 to 74 mm.; dotted line, result of suddenly increasing intensity from 0.25 to 12 ft-c.

Nipping increases with increasing light (Fig. 3) up to approximately 2.5 ft-c., and above this there is a deceleration and a levelling of the line at 4 ft-c. It should be emphasized that the light intensities here are comparable to early morning or late evening intensities in nature where midday illumination often reaches 10,000 ft-c. The effect of very bright light on nipping remains to be studied.

Seasonal Variation of Aggressive Behavior

Observations made in 1952 and 1953 indicated that aggressiveness was less prevalent in March and April than in the preceding months. The decline could be due to increasing seasonal light or temperature, and/or modifications related to the age of the fish. The phenomenon might be analogous to behavior changes at the time of smolt transformation of coho (5). Laboratory conditioning or diet might also be involved. However, additional fish brought to the University from Cultus Lake Hatchery in March, 1953, also showed a low degree of aggressiveness.

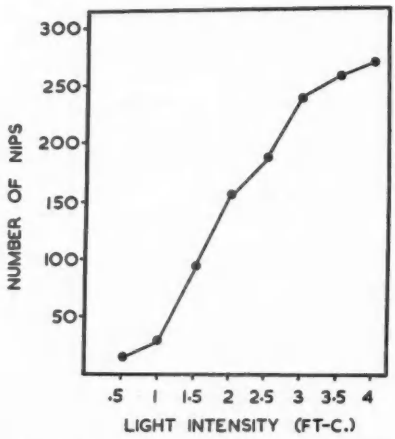

FIG. 3. Effect of increasing illumination (see legend Fig. 2).

Data presented in Fig. 4 were compiled over a seven month period (1953–54) and are based on 86 hourly observations. Again a marked decline occurred in April although this was less spectacular than that previously observed. Comparable experiments in 1953 show a decline in average hourly nipping rate from values between 100 and 200 in the autumn and winter to 14.4 during April. Water temperatures were lower in 1954 and this may have been responsible for the differences observed. Unfortunately a number of fish died from unknown causes toward the end of April, 1954, and it was necessary to terminate the experiment rather unsatisfactorily.

Releaser

Innate behavior patterns are "triggered" by sign stimuli or releasers such as color pattern, odor, shape, movement, mechanical stimulation, or some combination of these (10). Live fish of different species and models of various types were used in an effort to isolate the releasing mechanism for aggressiveness in trout. Since aggressive behavior disappears at low light intensity, it seems reasonable to assume that the sign stimulus is visual in nature, and all evidence obtained confirms this assumption.

Conclusions concerning the releasing mechanism are based on observations of (*a*) groups of trout containing individuals of different size, (*b*) behavior of trout with respect to other species of fish of comparable size, and (*c*) use of models.

Size in Relation to Aggressive Behavior

In a series of experiments involving 15 hr. of observation the six trout in any group consisted of two large individuals (6–6.5 cm.), two medium-sized

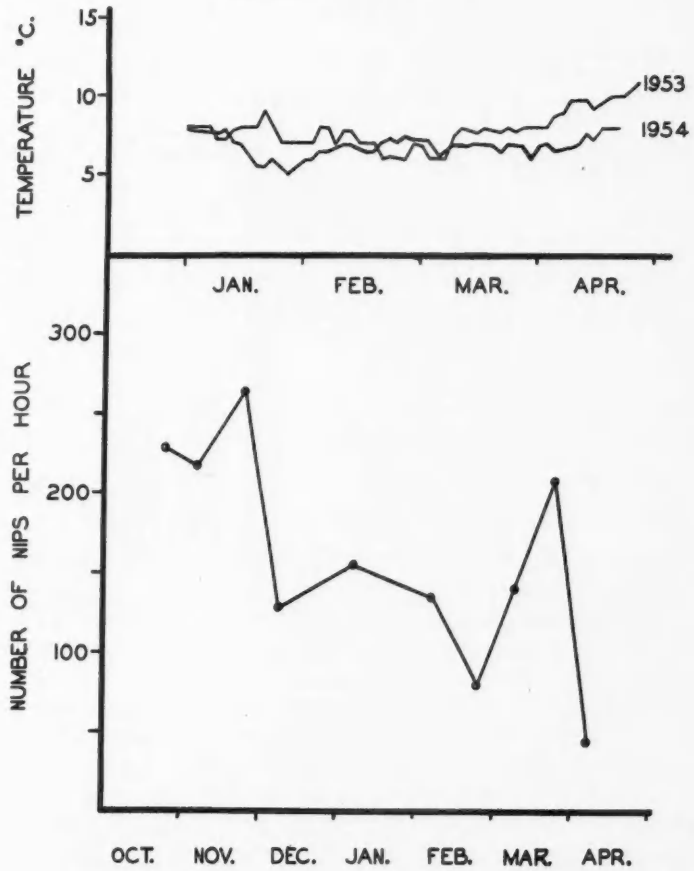

FIG. 4. Seasonal variation in aggressive behavior (1953–54).

individuals (5–5.5 cm.), and two small ones (4–4.5 cm.). A total of 1220 nips was recorded. In 762 cases a larger fish attacked a smaller one, in 223 cases the attacker and attacked fish were of equal size, and in 235 cases a smaller fish attacked a larger one. Thus it is evident that the larger fish were more aggressive. Conversely it may be stated that smaller individuals of a group release aggressive activities in the larger individuals to a greater extent.

In these experiments it was apparent that larger fish defended larger territories. Coho fry also show this relationship. Pertinent data for homotypic groups of trout or coho are summarized in Fig. 5. Large coho held about 45% of the total area of the aquarium while small members held 26%. Large trout held about 47% of the total area and small individuals about 17%.

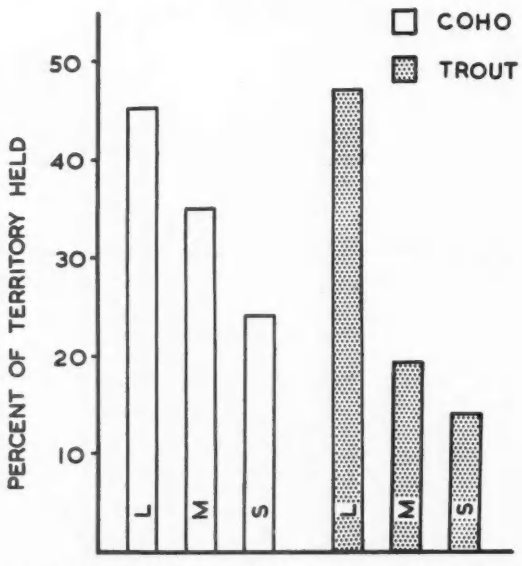

FIG. 5. Relation of size of fish to size of territory in homotypic groups of juvenile coho or trout; percentage calculated from length of tank area patrolled by aggressive large fish, *L*; medium-sized fish, *M*; or small fish, *S*.

Mixed Groups of Fish

In these experiments six trout were usually associated with five fish of some other species. Thus, any trout had an equal opportunity, so far as numbers are concerned, to attack another trout or the "foreign" species. By the use of live fish it was possible to obtain considerable variation in form, coloration, and activity. The following were available at one time or another: calico bass (*Pomoxis nigromaculatus*), stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), peamouth chub (*Mylocheilus caurinus*), squawfish (*Ptychocheilus oregonensis*), coarse-scaled sucker (*Catostomus macrocheilus*), goldfish (*Carassius auratus*), and coho salmon (*Oncorhynchus kisutch*). In addition tadpoles were used. The data, summarized in Table II, show that all fish and the tadpoles were attacked at some time by trout. However, certain species were more frequently attacked and a careful study of Table II suggests certain characteristics of the releaser.

Coloration is evidently an important component of the sign stimulus. "Orange" goldfish were rarely nipped while by comparison the black goldfish were nipped about seven times as often. Since sizes were comparable and movement was similar, the greater releasing value of the darker color seems evident. On the other hand, color pattern, shape, and spotting of fins and body did not seem particularly important. Uniformly colored squawfish and parr-marked spotted coho were nipped with about equal intensity.

TABLE II

AMOUNT OF NIPPING BY SIX TROUT IN HETEROTYPIC GROUPS. NUMBERS IN BRACKETS REPRESENT NUMBER OF TIMES TROUT ATTACKED TROUT

Species	Number of "foreign" fish	Fork length in cm.	Time observed (hr.)	Number of nips
Calico bass	5	4.4–5.1	6	45 (663)
Squawfish	5	3.8–7.1	7	666 (601)
Coho	5	4.8–7.2	16	831 (838)
Goldfish (orange)	5	3.8–4.6	6	103 (1040)
Stickleback	5	5.0–6.1	2	16
Prickly sculpin	4	4.5–6.5	2	21
Peamouth chub	6	5.0–6.0	2	71
Sucker	5	3.5–4.5	2	67
Goldfish (black) Goldfish (orange)	3 + 3	3.7–4.9	4	133 18

Certain fish such as calico bass and stickleback were rarely attacked although they are similar in color to other species which elicited frequent attacks. Type of movement and amount of movement are probably responsible for the differences. Species rarely attacked were those which remained quiet for long periods. Active species such as squawfish, coho, chub, and suckers elicited about equal numbers of attacks. Tadpoles and sculpins frequently rested on the bottom and were only nipped when they swam. Crappies and sticklebacks hang virtually motionless in the water for minutes, changing spatial position by short darting movements, and were less frequently attacked than squawfish and coho which were usually cruising about. The fact that a dead trout was not nipped when motionless while a dead trout on a moving wire elicited attacks (see below) is further evidence of the importance of movement in releasing aggressive behavior.

Models

Wooden models of different colors and shapes (Fig. 6) were placed in the aquarium and operated manually or mechanically. Manually operated models were suspended on one end of a steel wire with the other end of the

FIG. 6. Diagram showing type of model used to elicit nipping in trout. Various colors were used (× 2).

wire fused into a piece of glass tubing so that the models could be manipulated from behind a screen. By twisting the glass rod a model would describe an arc in the water. This method is subject to considerable bias for it is natural to try to entice an attack when a fish, especially an aggressive one, is near. Consequently no attempt was made to obtain quantitative data.

Models were suspended from a belt by a piece of steel wire and moved mechanically by a set of pulleys driven by an electric motor. In this experiment the models travelled slowly (0.2 ft. per sec.) around the periphery of the aquarium and action was limited to forward movement in a straight line about two inches under water. Models were observed for 15 min. while they were stationary and for the same length of time when moving. Because of similarity of data between mechanical and manually operated models, results are given for the former only.

Models (4–6 cm. long) of each of the following colors were observed separately for a period of three hours in an aquarium containing six trout (numbers following model color indicate number of attacks made on moving models): red—3, orange—0, green—5, blue—3, brown—6, brown with "trout" marking and white stomach—25, black—4, yellow—3, white—11, and dead trout—29. Motionless models were never attacked. Since these experiments were carried out over a period of time and involved several different groups of fish the quantitative data are not strictly comparable. However, the observations show clearly that movement is a primary requisite eliciting nipping. Since releasing value of models was lower than that of live fish, it can perhaps be assumed that the type of movement is also of significance to the fish.

Discussion

Aggressive behavior, like other behavior patterns, is dependent upon a requisite internal physiological state and an external releasing stimulus (10, 11). It has been postulated that the internal physiological state is dependent upon an "accumulation of action specific energy". The present study can contribute little to this aspect of the picture. Two features, however, may be of interest.

In the first place, the internal physiological state evidently develops less frequently during late winter and early spring than it does earlier. It seems likely that seasonal changes in activity of the endocrine glands are involved. These fish were too young to show sexual maturation but a seasonal spring-time increase in thyroid activity is characteristic of young salmon and changes in the pituitary activity resulting from photoperiodic stimulation are probable (6).

In the second place, it is evident that one or two fish in a group experience an "accumulation of action-specific energy" of this type while others either

do not experience such an accumulation or are prevented from expressing the behavior by unknown factors. That some fish in a group never or rarely show aggressive behavior might be due to difference in internal physiological state or due to a suppression of their behavior. Observation supports the latter view. When the dominant fish is removed from a group another fish will assume the role of aggressor. Similarly, when the second dominant fish is removed another fish will "take over" control. In some birds (1), learning seems to be involved and this might also be true of trout. Inhibitory interaction between drives is common in innate behavior (11) and the presence of an aggressive fish appears to increase the flight response and at the same time greatly reduces any attacking tendencies of other members. When a dominant fish is removed the nipping activity of non-aggressive fish increases until a new dominant is established.

The most interesting questions arising from experimental observations of this type concern the importance and significance of these activities in nature. Trout are often seen nipping and chasing in the streams where they live and it is reasonable to assume that this behavior has, during the course of its evolution, acquired vital importance for the juvenile trout. Tinbergen (11) emphasizes the role of this kind of behavior in forcing individuals apart. This spacing out of individuals results in the fullest utilization of "indispensable objects" such as food, space, or mates and at the same time provides better protection from predators. Larger and more aggressive fish have been observed to grow faster than small ones (3) or to have better access to the available food (9).

In trout territorial behavior may also be important in maintaining residence in rapidly flowing streams. At night, trout, like coho salmon (5), settle to the bottom, and nipping ceases. The nocturnal settling keeps the young fish in one locality during the night while territoriality keeps them in one locality during the day. Thus, it would seem that the variable periods which different species of Salmonidae spend in the streams depend on their relationship to the bottom and the intensity of their aggressive behavior (6, 7). Strongly schooling species show no relation to the bottom and leave streams early while very aggressive species, such as some of the trout, may remain permanently in the streams.

Acknowledgments

P. A. Larkin, Chief Fisheries Biologist for the Provincial Game Department, has provided financial assistance and helpful criticism. F. Pells, Fishery Officer at the Cultus Lake hatchery, has given every assistance in supplying fish. W. G. Smith prepared the sketches in Fig. 1. P. A. Larkin and Murray Newman criticized the final manuscript. It is a pleasure to express our thanks for this co-operation and assistance.

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CYTOLOGY AND PARTHENOGENESIS OF THE WHEAT STEM SAWFLY, *CEPHUS CINCTUS* NORT. (HYMENOPTERA: CEPHIDAE)[1]

By Margaret Rowlatt Mackay[2]

Abstract

A chromosome complement of 18 was established for the female of *Cephus cinctus* Nort. by counts of 18 elements at oogonial metaphase and nine bivalents at pachytene. The male has a haploid set of nine chromosomes on the basis of counts at spermatogonial metaphase and at meiotic metaphases I and II. Male haploidy was confirmed by the fact that the male karyotype comprises one member of each morphologically identifiable pair present in the female. Spermatogenesis is characterized by lack of synapsis and complete abortion of the first meiotic division. Formation of a monopolar spindle at first meiotic metaphase is discussed. A cytological comparison of thelyotokous and arrhenotokous strains of *C. cinctus* failed to reveal any difference in chromosome number or in chromosome morphology. *Cephus cinctus* reproduces largely by arrhenotoky, the population normally being bisexual; the males develop from unfertilized eggs, most of the females arising from fertilized eggs; azygous, or impaternate, females occur sporadically. From the bisexual population a thelyotokous strain has arisen that is not distinguishable by cytological comparison; the females of both arrhenotokous and thelyotokous races are diploid; no diploid males were found. The haplo-diploid relationship of male to female was confirmed; male haploidy has become established by adaptive modifications in meiosis, as indicated in the cytological details given.

Introduction

In 1934 the wheat stem sawfly, *Cephus cinctus* Nort., which is indigenous in the Great Plains of North America, became a serious economic pest of wheat in the southern part of Alberta (Farstad (5)). Studies on biology and control revealed both bisexual and unisexual populations of *C. cinctus*. The economic implication of the occurrence of a female-producing strain was recognized. As a measure of its biological significance, the parthenogenetic behavior and cytology of the unisexual as compared with the bisexual populations were investigated. This paper is a report on the investigation.

Cytology

Reproduction in Hymenoptera is largely haplo-diploid, or arrhenotokous, as the males develop from unfertilized, haploid eggs and the females from fertilized, diploid ones. Thelyotoky (the production of females by diploid parthenogenesis) is known to coexist with arrhenotoky in the same group, or even in the same species (White (28)). In the Symphyta, arrhenotoky is the rule in most species. However, thelyotoky coexists with arrhenotoky in a few species (Peacock (16), Sanderson (19), Smith (25)), and in several species thelyotoky is complete (Benson (1)).

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The cytology of reproduction in the leaf-feeding Hymenoptera (Symphyta) has been investigated by Comrie (2), Doncaster (3, 4), Greenshields (6), Gresson (7), Peacock (15, 16), Peacock and Gresson (17), Peacock and Sanderson (18), and Smith (24, 25, 26). Male haploidy and female diploidy were demonstrated and in no case were sex chromosomes distinguished. In species exhibiting facultative parthenogenesis, oogenesis is normal and spermatogenesis is characterized by a lack of synapsis and by an abortive first meiotic division. In the second meiotic division of the male the chromosomes divide by simple mitosis, two functional spermatozoa forming from each spermatocyte. Smith (25) found that, although exceptional spermatocytes in *Diprion hercyniae* (Htg.) (*Diprion polytomum* Htg.) have a diploid number of chromosomes, the chromosomes do not pair and the first meiotic division is aborted as in the normal haploid male. The special type of meiosis found in some hymenopteran males is therefore genetically determined and is not a direct result of male haploidy (Whiting (30, 31), Smith (25)).

Materials and Methods

The cellular development of the gonads and, then, the chromosome pattern in both sexes were determined as follows. The chromosomes of the gonia were obtained from squash preparations of larval gonads. Spermatocyte and oocyte nuclei undergoing meiosis were found in individuals just before and after metamorphosis from larva into pupa. Spermateleosis was traced in young, unpigmented pupae, and the sequence of development of the ova was shown in the pupal ovaries. The large majority of somatic preparations were made from the nuclei of ovarian follicle cells of the pupa; these contained the largest chromosomes of any tissue examined.

For the most part the aceto-orcein smear technique, first described by La Cour (12), was used. Storage of the insects at 0° C. overnight before dissection improved the stainability of the tissue. Dissection was carried out in Ringer's solution, the tissue then being transferred to a drop of 15% acetic acid on a slide. A few drops of aceto-orcein were added and the material was left to stain for 15 min. before being squashed. Repeated gentle heating of the slide over steam and light pressure on the cover slip drove most of the stain from the cytoplasm, thereby improving the definition of the chromosomes. Some squash preparations of the larval gonads were fixed in modified Kahle's fixative and stained by the Feulgen method as described by Smith (27).

To supplement information gained from an examination of squashed material, gonads were sectioned at 6 and 8μ and stained with Heidenhain's haematoxylin, the Feulgen method, or crystal violet (after Newton) counterstained with fast green. Although the chromosomes were too small for critical study in this material, the sections gave information on the orientation of the cells in the gonads and on spindle formation within the cells, and were particularly valuable in tracing the development of the oocytes.

Total mounts of pupal ovaries prepared by Whiting's (29) method were valuable in investigating the progressive development of oocytes. The same technique was applied to unlaid eggs of the mature female.

The photographs were taken with a Leitz Makam, with a Wratten filter No. 61. The sectioned material was photographed at a magnification of 440× and the squash material at 900×. Drawings were made at table level with an Abbé-type camera lucida at magnification of 3000× and 4500×.

Spermatogenesis

The paired testes of a mature larva are in the fifth abdominal segment and are at most 0.5 mm. in length. To distinguish between male and female larval gonads, three morphological criteria were employed. The testis usually comprises six locules, whereas the ovary normally contains seven ovarioles. The larval testes are noticeably more dense than the female organs, and the locules are shorter and broader. Also, as shown by Dr. N. D. Holmes of the Lethbridge laboratory, there is a small swelling in the suspensory ligament close to the gonad of the female larva, but not in the male.

Upon completion of feeding, the larva enters a diapause. Growth and division of the cells of the gonads continue slowly throughout diapause. When the testis reaches a length of 0.8 to 1.0 mm. a sticky, non-cellular covering is elaborated, causing a large apparent increase in size of the gonad. In the preparation of squashes, removal of this envelope is imperative to ensure staining of the cells.

At the time of metamorphosis into the pupa there occurs a second noticeable increase in size of the gonads, caused by mitotic multiplication of cells. Length is doubled to approximately 2.0 mm. in the six or seven days required to transform larva into pupa.

These differences in size and morphology make it possible to associate accurately the stage of germ cell development with the age of the immature insect. Testes of early diapause larvae contain spermatogonia in eight-cell cysts as well as germ cells in earlier stages. Meiotic divisions are found in the testes of larvae that exhibit the external morphological characteristics termed "prepupal" and in the testes of early pupae. The division of spermatocytes into spermatids is initiated with the metamorphosis into the pupal stage. Development of the spermatozoa is completed during the pupal stage and sperm bundles move down the vas deferens to be stored in the seminal receptacle, as shown by Dr. N. D. Holmes at the Lethbridge laboratory. Adult testes are degenerate structures, empty except for follicle and interstitial cells and perhaps a few degenerating germ cells.

Early pupae are most satisfactory for the study of spermatogenesis, as all stages from gonia to immature spermatozoa are present. There is a definite seriation of stages from the proximal to the distal end of the testis (Fig. 1).

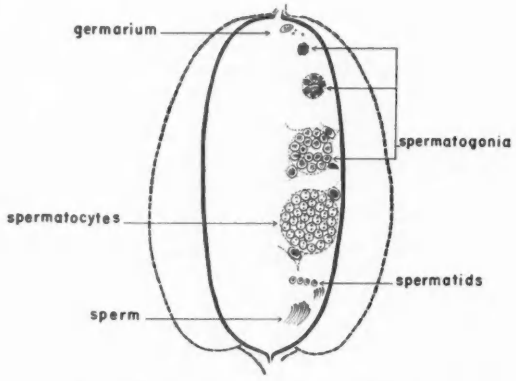


FIG. 1. Diagrammatic longitudinal section of the relative arrangement of the germ cells in the early pupa of *C. cinctus* male.

Spermatogonia

The youngest gonial cells are compactly arranged in tight rosettes so that the individual cells are wedge-shaped. As the gonia grow, the chromatin becomes arranged in clumps about the periphery of the nucleus. The cells of each group become more loosely associated with each successive division, although they retain "interzonal" connections until the third generation, when each germ cell has divided to give eight gonia. After the fourth mitotic division, the 16 resultant gonia lie free within each cyst (Fig. 3). Each cyst in the larval testis just before pupal metamorphosis encloses 32 spermatocytes, the product of five mitotic generations.

The cells within each cyst divide synchronously. Each cell division is followed by a period of growth. At any one time the majority of cysts always contain cells with the relatively diffuse distribution of chromatin characteristic of interphase. The relative frequency of cysts in the various phases suggests that the gonial divisions proceed rapidly. Counts from 72 metaphase figures establish the chromosome number as nine (Fig. 2*a*); deviations of one chromosome were found in only three.

The connective tissue elements of the larval testis include three types of cells, which differentiate at the same time as the gonia. These are the follicle cells, which make up the epithelial covering of the testicular locules; the cyst wall cells, which separate the groups of gonia; and the interstitial cells, which occur in the corners between the cyst walls. The interstitial cells are nine to 10μ in diameter in sectioned material as compared with 8 to 9μ for the germ cells. They usually contain one nucleolus but may have two. Occasionally, cells considerably larger than either germ cells or interstitial cells were observed within the cysts. Dr. P. W. Whiting of the Department of Zoology, the

University of Pennsylvania, suggested to the writer that these are polyploid cells that have failed to divide properly and are of no significance in the normal spermatogenetic process. This suggestion is supported by the occurrence of some pairing of the chromatin clumps in *C. cinctus*. Although their fate and function are open questions, it was evident that the polyploid cells did not transform into spermatids in the material studied.

Spermatocytes

The spermatocytes, products of the fifth spermatogonial division, show little if any difference in size from cells of the preceding generation. After a short resting phase, chromatin begins to condense about the periphery of the nucleus in a manner similar to that in the early spermatogonia. Since the chromatin becomes dispersed throughout the nucleus once more before the chromosomes are defined, these chromatin condensations, which number approximately nine, may actually be prochromosomes.

An intervening resting phase is followed by the reappearance of the chromosomes as discrete bodies. No synapsis occurs in the prophase thus initiated. Condensation of the chromatin progresses until metaphase, at which time the chromosomes are unmistakably meiotic, being shorter and thicker than at mitotic metaphase. Although no synapsis has occurred, the first metaphase chromosomes are obviously double (Figs. 2*b*, 4*a*, and 5*a*) in preparation for the equational split. A monopolar spindle now forms and the chromosomes become oriented, the kinetochore of each pointing to the single pole (Fig. 2*c*). Chromosome fibers can be seen connecting the kinetochores and the single pole. These fibers do not appear to shorten and most of the chromosomes do not undergo a noticeable anaphasic movement on the unipolar spindle. Figures were found, however, (Figs. 2*d* and 2*e*) that suggest that one chromosome does move alone toward the pole. As no confirmation of anomalous behavior on the part of any single chromosome was found elsewhere during the meiotic cycle, special significance is not now attached to this observation. The nuclear membrane does not break down during the first meiotic "division", nor is there a division of chromosomes or of cytoplasm. The first division is therefore completely abortive. The telophase chromosomes gather into a dense, compact mass during a short interkinesis (Fig. 2*f*). The chromosomes re-emerge in prophase configurations of the second division (Fig. 2*g*). A bipolar spindle then forms and the nine dyads become arranged on a true metaphase plate (Figs. 2*h* and 2*i*). This spindle lies at right angles to that of the abortive division. At anaphase, nine elements pass to each pole (Fig. 2*j*), confirming the absence of reduction during meiosis. At telophase the chromosomes mass together in a tight knot (Fig. 2*k*). The nuclear membrane now forms, and immediately thereafter the chromosomes lose their definition in a typical interphase of short duration.

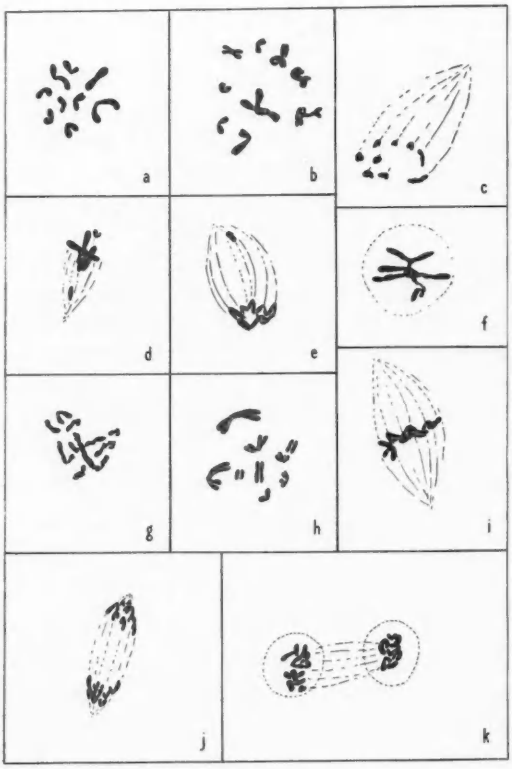


FIG. 2. Spermatogenesis in *C. cinctus:*
a, spermatogonial metaphase; *b*, first meiotic metaphase, polar view; *c*, first meiotic metaphase, side view; *d* and *e*, anaphasic configurations; *f*, interkinesis; *g*, prophase of the equational division; *h*, second meiotic metaphase, polar view; *i*, second meiotic metaphase, side view; *j*, equational division, second anaphase; *k*, telophase.

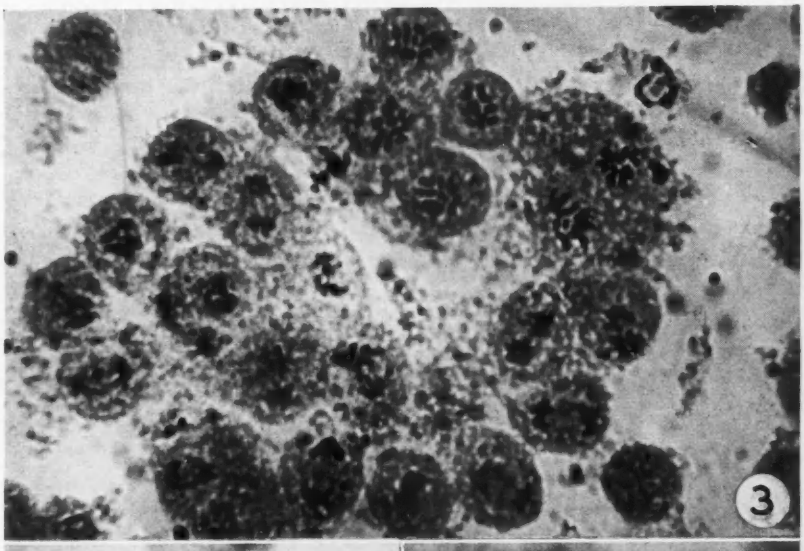
Spermateleosis

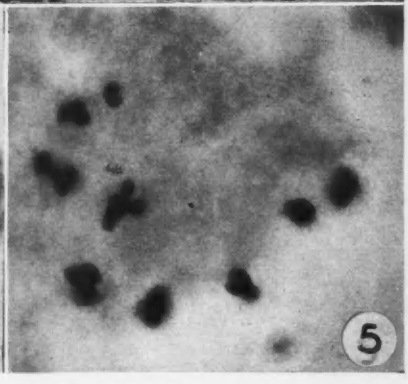
After the meiotic division, various characteristic changes occur in the daughter cells (spermatids), transforming them to spermatozoa (Figs. 6 and 7). The chromatin clumps into small aggregations and moves to the periphery of the nucleus. This change is accompanied by a gradual lengthening of the cell, the nucleus remaining at one end. Most of the chromatin moves toward the edge of the nucleus near the point where the flagellum can be seen to be differentiating within the spermatid. Blunt projections then develop at both

FIG. 3. Cysts of fourth generation spermatogonia with chromosomes in metaphase and anaphase. Acetic-orcein. 420×.

FIGS. 4 and 5. First meiotic metaphase chromosomes of the male. Acetic-orcein. 2700×.

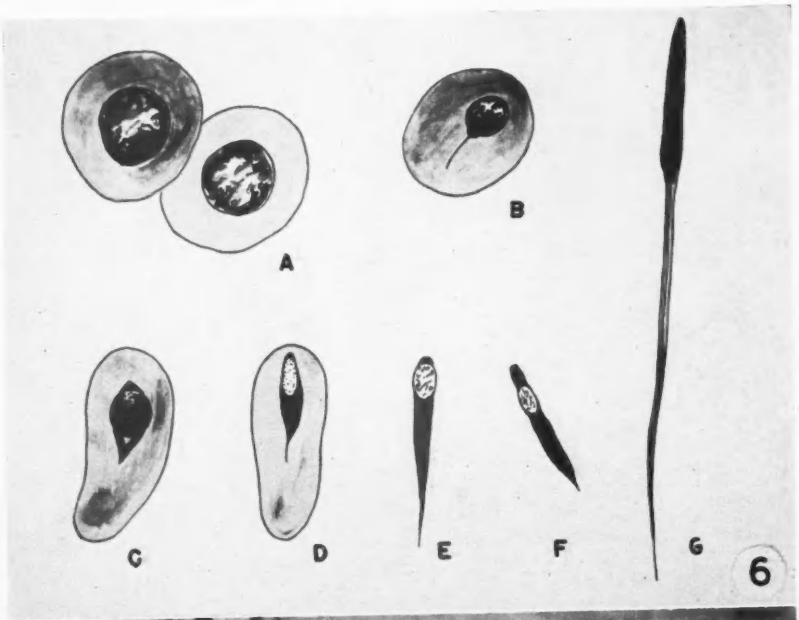
FIGS. 4*a* and 5*a*. Camera lucida drawings of the metaphase chromosomes of Figs. 4 and 5, respectively.





4a

5a


A
B
C
D
E
F
G
6

7

anterior and posterior ends of the nucleus, giving the nucleus a characteristic ellipsoidal shape. Elongation of the cell attends the transformation of the spermatid nucleus.

Each spermatid completes the changes to spermatozoon within one week. Sixty-four spermatozoa are arranged in each cyst so that the heads all face in one direction but not necessarily toward a duct. They are simple flagellate sperm consisting of head, middle-piece, and flagellum. The two centrioles remain at the base of the nucleus in the middle-piece. The flagellum is sheathed throughout most of its length, leaving only a short end exposed. In sectioned material fixed in Flemming's fixative and stained in crystal violet, the head and neck region of the sperm measures approximately 7μ. The flagellum, by comparison, is 20μ long.

Oogenesis

Histology of the Ovaries

The ovarioles are polytrophic, oocytes alternating with groups of nurse cells in the maturing ovary. The rudiments of at least seven eggs can be seen in each of the seven ovarioles of an ovary, but only three of these eggs reach maturity during the adult life of the sawfly. The egg-laying potential was estimated at an average of 40 eggs. As shown by Dr. N. D. Holmes of the Lethbridge laboratory, the mature eggs pass down the oviduct to be stored in the calyx after the adult has emerged.

As in the stage of development of the larval testes when the mucilaginous sheath is proliferated, there is a point in the development of the larval ovaries that can be used as an aid in associating the external appearance of the gonads with the stage of development of the cells. Squash preparations from the ovaries of female larvae at this stage show oogonial mitoses in abundance, and slides prepared of testes of a comparable age contain spermatogonial mitoses. At this point the ovaries are 0.8 to 1.0 mm. long, and each ovariole contains at least one differentiated oocyte that has attained a sufficient size to cause a noticeable swelling about two-thirds of the distance from the anterior end of the ovariole to the posterior. Between this swelling and the tip of the ovariole are a number of small cells that are destined to become the lateral oviducts and calyx.

After the last oogonial division the oocytes become differentiated from the nurse cells. The chromosomes of the nurse cells undergo synapsis as do those of the oocytes, indicating that the nurse cells are essentially aborted ova and have a common origin with the egg cells.

The oocyte is gradually walled off by follicle cells, which finally spread out into a layer one cell thick (Fig. 8). The separation of the oocyte from the nurse chamber by the follicle cells is not complete (Fig. 9) and, as the oocyte

FIG. 6. Spermateleosis in *C. cinctus:*
a, sister spermatids; *b* to *f*, transition from spermatid to spermatozoa; *g*, mature spermatozoon.

FIG. 7. Spermatid nuclei and immature sperm of *C. cinctus*. Acetic-orcein. 850×.

develops, a flow of some substance or substances occurs posteriorly from the chamber into the cytoplasm of the immature egg. This substance stains with a cytoplasmic stain (fast green) and does not stain with crystal violet. The nurse cells may be "used up" in the process, for no nurse cells are visible between the last two eggs in the ovarioles of sawflies ready to emerge.

At the time of pupal metamorphosis in the female sawfly, there is rapid growth and elongation of the ovarioles. The increase in size is due primarily to the growth of the cytoplasmic portion of the developing oocytes. In terms of nuclear development, the prepupal stage of the female can be associated with the synaptic stage of meiotic prophase.

Oogonia

The early gonial cells are not distinguishable from those of the male. They, too, are bound together in rosette formation, each rosette comprising the descendants of one primary germ cell. Cell division proceeds normally in the ovaries but only four generations of gonia are produced, in contrast to five in the testes. Oogonial metaphase figures clearly show the diploid number of 18 chromosomes as compared with the haploid number of nine seen in the spermatogonia.

Growth of the Oocyte

After the last oogonial division, one of the most posterior of each group of 16 cells differentiates into an oocyte and the others become its nurse cells. Synaptic figures are found in recently differentiated oocytes; in these, nine bivalents are countable, representing the 18 synapsing elements (Fig. 10). The nucleolus is associated with one of the shorter pairs. Fig. 11 shows a section through a portion of two prepupal ovarioles with three differentiated oocytes whose nuclei contain synapsing chromosomes. Coincident with the ensuing rapid growth of the cytoplasmic contents of the oocyte, the chromosomes after pachytene seem to expand and become fuzzy in outline like "lampbrush" chromosomes. These chromosomes have not been shown with acetoorcein, crystal violet, the Feulgen method or Heidenhain's haematoxylin after pachytene, although the nuclei of both nurse and follicle cells continue to react visibly to the stain.

As the oocyte grows, the germinal vesicle moves from the center of the cell toward the wall. Bodies similar to those described as "accessory nuclei" in the literature appear close to the egg nucleus during the latter part of the growth period but before the yolk is laid down (Fig. 12). These bodies are Feulgen-negative and therefore do not contain chromosomes. These secondary nuclei disappear at the time of formation of the yolk in the maturing oocyte.

By the end of the growth period, when the deutoplasm is being laid down, the nucleus is close to the follicle layer in the anterior third of the developing egg (Fig. 13). The yolk granules are not homogeneous and they show different staining properties; some granules retain a gray coloration after osmic fixation and are therefore probably of a fatty nature.

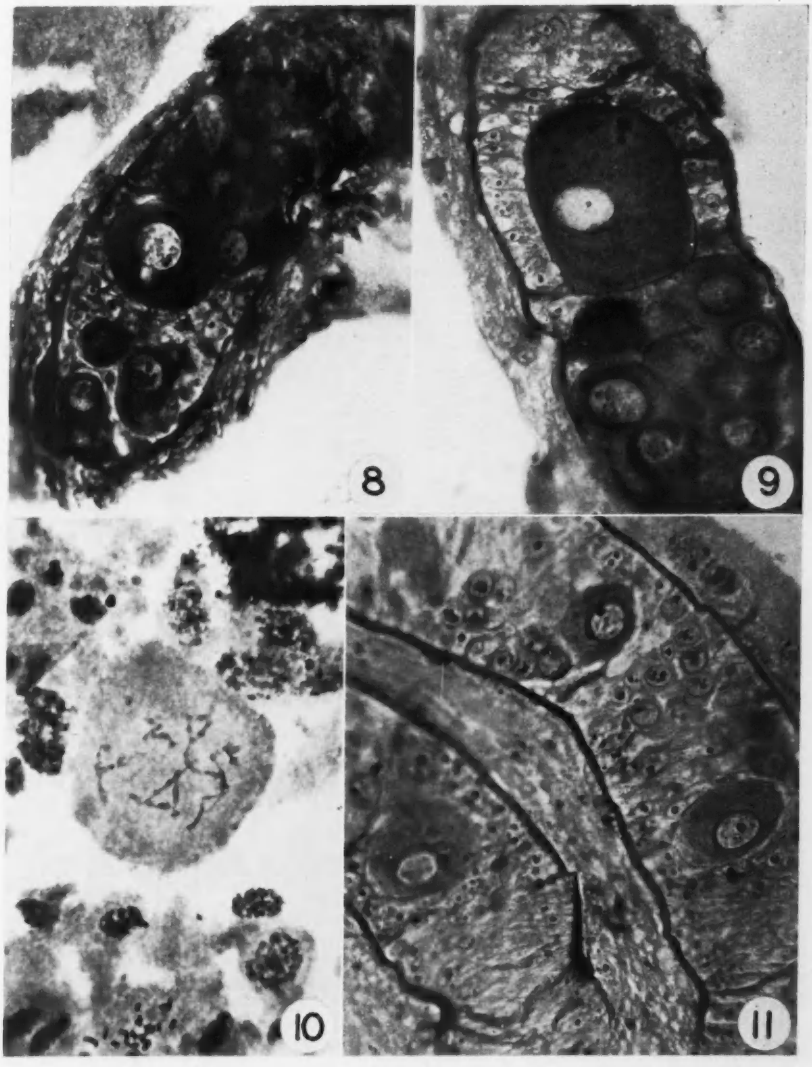
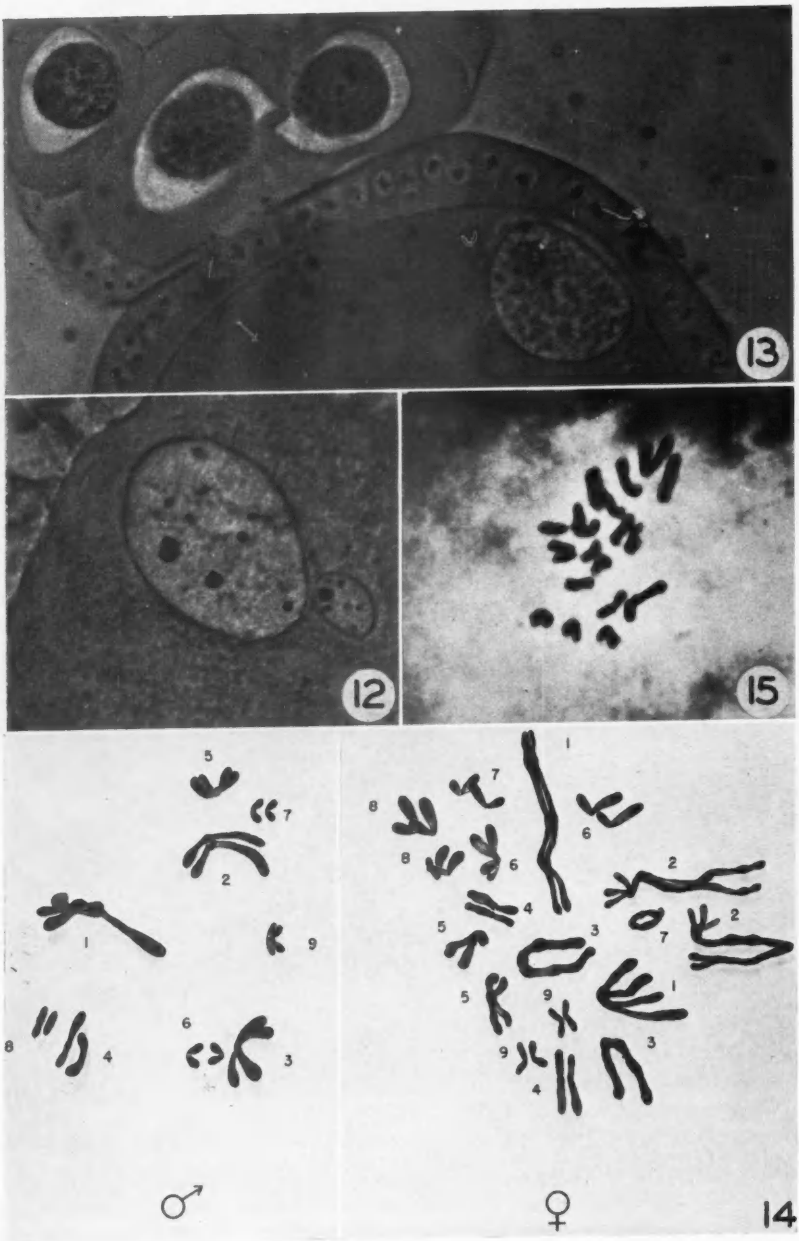


FIG. 8. Follicle cells are seen to begin the walling-off of a differentiated oocyte with its nurse cells. Heidenhain's haematoxylin. 440×.

FIG. 9. A single layer of follicle cells finally surrounds the oocyte but does not separate it posteriorly from its nurse cells. Heidenhain's haematoxylin. 440×.

FIG. 10. Synapsis in young oocyte nucleus, showing nine bivalents. Acetic-orcein. 900×.

FIG. 11. Section through two prepupal ovarioles with three differentiated oocytes. Heidenhain's haematoxylin. 440×.


13
12
15
♂
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14

Meiosis progresses as far as first metaphase before the egg is laid. If the female is not allowed to oviposit, anaphase configurations are found in eggs dissected from the abdomen after several days. Meiosis, however, proceeds no further than anaphase in eggs retained within the female body. The further course of maturation of the egg after oviposition has not been investigated.

Chromosome Number, Morphology, and Size

As shown in the description of the chromosome cycle in *C. cinctus*, the chromosome number is nine in the male germ-line and 18 in the female. The most convincing evidence for this haplo-diploid relationship was obtained from a comparison of a large number of male and female gonial cells. Absence of synapsis in the spermatocytes is understandable as a corollary of male haploidy. In Fig. 14 the chromosome complement of the male is compared with that of the female. In the female complement the chromosomes can be paired; comparison with the haploid male figure shows that the latter contains one member of each pair present in the female set.

The nine chromosomes of the basic complement are metacentric, and three of the nine can be identified readily in somatic metaphases and anaphases and in meiotic metaphases I and II in the male. The largest chromosome is definitely J-shaped. The next largest is V-shaped, with a characteristic achromatic section on one arm near the centromere. The third largest is also V-shaped, with deeply staining areas on either side of a median centromere. There are two slightly smaller metacentric chromosomes and four small metacentric chromosomes, of which one sometimes appears to be smaller and more lightly staining than the others. The six smaller chromosomes cannot be distinguished accurately one from the other.

The Somatic Chromosomes

Somatic mitoses were studied in tissue from neural ganglia, Malpighian tubules, follicle cells of the gonads, and wing buds of individuals near pupal metamorphosis. Whereas the chromosome number in the cells of the germ-line is constant, the number does vary in the somatic tissues and polyploidy is common. Cells of the neural ganglia of the male contain a chromosome complement of nine, and those of the female 18. The chromosome count in these cells is uniform. Polyploid cells up to octaploid were found in tissue from the wing buds and the Malpighian tubules. Polyploidy is also evident in the epithelial cells of both male and female gonads. The tissues in which

FIG. 12. Accessory "nuclei" arise from the germinal vesicle during the latter part of the growth period. Newton's crystal violet. 1000×.

FIG. 13. The egg nucleus has reached a position in the anterior third of the developing egg near the follicle layer by the end of the growth period. Newton's crystal violet. 440×.

FIG. 14. Haploid and diploid chromosome sets of male and female in *C. cinctus*.

FIG. 15. Female somatic metaphase; ovariole follicle cell of pupa. Acetic-orcein. 2700×.

polyploidy occurs are involved in rapid growth and development. The ovarian follicle cells have the largest metaphase chromosomes found in any tissue and they have a normal diploid number of 18 (Fig. 15).

Chromosome Size

The size of the chromosomes varies greatly with the stage. At pachytene in the oocyte nucleus the largest chromosome is 16μ long and the smallest 6μ. The somatic metaphase chromosomes in the follicle cells of the pupal ovary range in length from 6 to 1μ, and the chromosomes of the male neural ganglia from 5 to 1μ. The spermatogonial metaphase chromosomes measure from 4 to less than 1μ in length. As is usual, the shortest chromosomes are those of the first meiotic metaphase in the germ-line of both sexes. In the spermatocyte the longest chromosome is only 2μ in length, the shortest 0.7μ. In the egg nucleus the metaphase chromosomes defy accurate measurement, being even smaller than the corresponding chromosomes of the male.

Comparison of Chromosomes in Arrhenotokous and Thelyotokous Populations

Somatic and germ-line chromosomes were examined in 53 females from the thelyotokous population and in 83 females and 200 males from the arrhenotokous population. The females of both populations have a diploid set of chromosomes as determined in oogonial counts. Thirty-five clearly analyzable metaphase plates were obtained from the thelyotokous females and 31 from females of the bisexual population. No noticeable morphological differences exists between the chromosome sets of the females from the two populations.

Discussion

The wheat stem sawfly follows the basic chromosome pattern established for primitive Hymenoptera. In the oogenesis of females exhibiting facultative parthenogenesis, pairing and chiasma formation take place in the usual manner. Females have two of each morphologically distinguishable chromosome of the haploid set and are therefore diploid. Of 200 males examined cytologically, none was diploid. Male haploidy has become stabilized by adaptive modifications of male meiosis, that is, absence of synapsis and suppression of the first division. This reduction of the meiotic process to a single equational division ensures the production of normal haploid spermatozoa.

The Monopolar Spindle

Monopolar spindles are by no means of common occurrence in the Insecta and the reporting of another case deserves special mention. Anomalous meiotic figures variously termed *monopolar*, *unipolar*, *half*, or *abortive spindles* have been described in a fly, *Sciara* sp. (Metz (14)), two lecanoid coccids

(Schrader (20, 21), Hughes-Schrader (10)), a beetle, *Micromalthus debilis* Lec. (Scott (22)), and several hymenopterons (Sanderson (19), Koonz (11), Smith (25)).

In the Hymenoptera, cytological difficulties in the critical study of meiotic cells have curtailed descriptions of the monopolar spindle and its possible significance. It is, however, always formed at the time of the abortive meiotic division in the male. Anaphasic movement of the chromosomes to the single pole has been reported. Smith (25) described a complete half-spindle in *Diprion hercyniae* (Htg.) that radiates from a centrosome near the nuclear membrane; all of the anaphase chromosomes move toward the single pole. In *C. cinctus* the limited chromosomal movement at anaphase is also toward the pole.

The available data on monopolar spindles in Hymenoptera do not warrant a stand being taken on the theoretical implications of a monocentric mitosis. It seems likely, however, that this mechanism in the Hymenoptera differs from that in *Sciara* sp., *Micromalthus debilis* Le Conte, or the lecanoid coccids. In *Sciara* sp. and *M. debilis* the anaphase chromosomes connected with the unipolar spindle move *away* from the pole. The hymenopteran chromosomes apparently move *toward* the single pole at anaphase, if they move at all, and there is no separation or segregation of the chromosomes. In the coccids, movement is toward the pole but chromosomes associated with the monopolar spindle are later discarded. The monopolar spindle of *Sciara* sp. is also associated only with chromosomes to be eliminated. In the Symphyta the chromosomes are all associated with the monopolar spindle and none of the chromosomes appears to be discarded. There is no evidence of a regular segregation of anaphase chromosomes on the monopolar spindle of the haploid males that have been examined (e.g., *M. debilis* and several hymenopterons). It seems likely, therefore, that the significance of the unipolar spindle in haploid males is not concerned with regular elimination of chromosomes.

Accessory Nuclei

The appearance of "accessory nuclei" during the growth phase of the oocyte is a phenomenon often reported in the oogenesis of the Hymenoptera. That these "nuclei" are extruded from the germinal vesicle has been demonstrated (e.g., Hegner (8), Hogben (9), Gresson (7), Sanderson (19)). Smith (25) described the budding-off and subsequent elimination through the nuclear wall of an extrachromatic substance from diakinetic bivalents of *Diprion hercyniae* (Htg.). In *C. cinctus* the origin of the eliminated material is not clear, although it certainly passes out through the wall of the germinal vesicle and is Feulgen-negative.

Parthenogenesis

For the last 20 years extensive surveys throughout the sawfly-infested area in Alberta and Saskatchewan have shown that the population of *C. cinctus* is largely bisexual. An exceptional, localized population, however, was reported

by Farstad (5) to reproduce by thelyotoky, i.e. diploid parthenogenesis. For eight years no males were found among large numbers of adult sawflies that emerged in the laboratory from collections made yearly in that locality; nor were any male sawflies found during the flight periods of the adult in the field. The first male sawfly found in that population was reported by Mr. W. A. Nelson, now of the Veterinary and Medical Entomology Section, Lethbridge. In 1949 and 1950, when collections were made for a cytological survey of the population, only one male among every 200 females was found in the field. On these grounds, the population was considered to be thelyotokous for purposes of this investigation. The unisexual population of this locality has been practically eliminated in the last two years by the concerted efforts of farmers in the district. Further investigation of the thelyotokous race is therefore not at present feasible.

Unfortunately it has not yet been possible to rear *C. cinctus* in the laboratory for genetic purposes. However, limited data have been obtained by the following procedure. Wheat stubs containing larvae from a bisexual population were collected in the field and individual stubs were isolated so that mating of the emerged adults could be controlled in the manner described by McGinnis (13). Some of the adult females were enclosed with males and observed to mate; other females were not allowed to mate. Each female was then transferred to a caged wheat stem and, after oviposition, that stem was marked and the female transferred to another stem. In this way a series of stubs was secured, each of which was labelled and stored, and when the adults emerged the numbers of male and female offspring were recorded. This experiment was carried on during three consecutive summers. Of the 67 viable offspring obtained from mated females, 48 were males and 19 females. Of 83 offspring from virgin females, 73 were males and 10 females. In 1953, Mr. L. K. Peterson of the Lethbridge laboratory reared offspring of a single virgin female to the third generation. He also found, confirmatory of the above experiment, that males usually arise from unfertilized eggs but that, occasionally, in the bisexual population females also arise from eggs that are not fertilized. Both male and female offspring are obtained from eggs laid by mated females; the males develop from unfertilized eggs by facultative parthenogenesis.

Discussion

Excepting the thelyotokous race, *C. cinctus* is largely facultatively parthenogenetic. Eighty-eight per cent of impaternate offspring in a bisexual population are haploid males. The other 12% are females, which are, presumably, azygous diploids. Eggs laid by mated females give rise to both male and female offspring, the females being normally zygotic. This population is evidently not of a single, stable, arrhenotokous type, as evidenced by the production of a small percentage of impaternate females. Such a population probably contains recessive male-determining factors together with genes determining parthenogenesis. It therefore could act as a reservoir for the

segregation of some combinations giving rise to impaternate females among the larger percentage of individuals of the arrhenotokous type.

In the thelyotokous population, unfertilized eggs develop into diploid females, the diploid chromosome number being regained presumably during the maturation of the egg, as has been shown in other thelyotokous forms (Sanderson (19), Smith (25)). Unfortunately none of the spanandric (rarely-occurring) males were examined cytologically but the possibility of occurrence of diploid males is considered to be slight. It is possible that thelyotoky in *C. cinctus* arose by mutation (Smith (23)) from an ancestral bisexual race that was indigenous in the native grasses. The nature of such a mutation must have caused diploid azygosity. Or the parthenogenetic race may conceivably have arisen also by natural selection among the descendants of sporadically occurring diploid azygotes arising from haploid parthenogenesis.

Acknowledgments

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INFLUENCE DU DÉRIVÉ CYANURÉ DU DDT SUR LE RYTHME CARDIAQUE DE *PERIPLANETA AMERICANA* (L.)[1]

PAR E. R. BELLEMARE[2] ET JEAN BELCOURT[3]

Abstract

The mode of action, on the heart of *Periplaneta americana*, of the cyanide analogue of DDT has been studied. Results of preliminary tests with rotenone confirm the findings of other investigators. Tests made with DDT produce a slight reduction of the cardiac rhythm. With the cyanide analogue of DDT, the rate of heart beat is also slightly reduced but, as with DDT, the pulsations continue long after paralysis has set in. The general intoxication symptoms produced by the injection of the cyanide analogue (in suspension) are likewise identical with those of DDT. The above results, together with results of experiments found in the literature, seem to be at variance with the hypothesis proposed by Krijgsman *et al.* that the heart mechanism of insects consists of a neurogenic pacemaker with adrenergic properties, controlled by a cholinergic accelerating nerve.

Introduction

Plusieurs chercheurs ont utilisé les variations du rythme cardiaque de l'insecte comme critère de l'action physiologique de certains insecticides. Quand un composé chimique accélère ou ralentit la fréquence des contractions, la question se pose si le composé agit sur le myocarde ou sur les cellules nerveuses associées au cœur, ou bien sur les deux. Cette question nous amène nécessairement à considérer l'automatisme cardiaque de l'insecte.

Deux théories ont cours au sujet du siège de l'automatisme cardiaque chez l'insecte. Pour certains physiologistes, la contraction est myogénique, pour d'autres, elle est neurogénique. McIndoo (9) montre histologiquement la présence d'éléments nerueux dans le cœur de la blatte. Coon (4), à la suite d'expériences avec la nicotine et la pyrèthre sur *Periplaneta americana* déclare que le contrôle neurogénique des contractions cardiaques est secondaire à l'action myogénique; il a en effet observé que le myocarde continue à se contracter rythmiquement longtemps après la paralysie totale des appendices. Duwez (6) a observé que le cœur isolé du dytique continue de battre spontanément et rythmiquement; cependant la fréquence des contractions diminue. Il en est de même si l'on divise le myocarde en fragments; chacun de ceux-ci se contracte spontanément. Les potentialités d'automatisme semblent présentes dans toute l'étendue du vaisseau cardiaque, et ce chercheur n'a pu localiser de centre prédominant de l'automatisme. Cependant Yeager (16) a observé que, chez *Periplaneta americana*, la partie du cœur située dans les segments abdominaux quatre ou cinq, se contracte avec une amplitude plus grande que dans les autres segments. Y aurait-il là une indication de prédominance ? On sait, par ailleurs, que le cœur de

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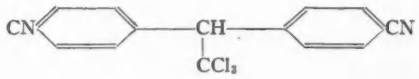
certains autres arthropodes se contracte rythmiquement sans l'influence d'aucun influx nerveux, ainsi que Maloeuf (10) l'a observé chex *Anax junius*, et Carlson et Meek (3) chez l'embryon de *Limulus* sp. alors que l'on ne peut même pas discerner un anlage d'élément nerveux.

A côté de cette théorie myogénique, il est intéressant de considérer l'opinion émise récemment par Krijgsman *et al.* (8). Ces auteurs ont étudié les effets d'une série de composés sur le rythme cardiaque et ont conclu que: (1) le mécanisme cardiaque de la plupart des arthropodes, et en particulier de *Periplaneta americana*, possède un *pacemaker* ou centre d'automatisme neurogénique avec transmission synaptique; (2) ce *pacemaker* a des propriétés adrénergiques; et (3) il est soumis à l'influence d'un nerf accélérateur cholinergique.

Avec ces deux théories présentes à l'esprit, nous avons observé l'influence du nouveau composé analogue au DDT, le 1,1,1-trichloro-2,2-bis-(*p*-cyanophényl)-éthane, sur l'appareil circulatoire de *Periplaneta americana*. Ce composé possède la structure chimique suivante:



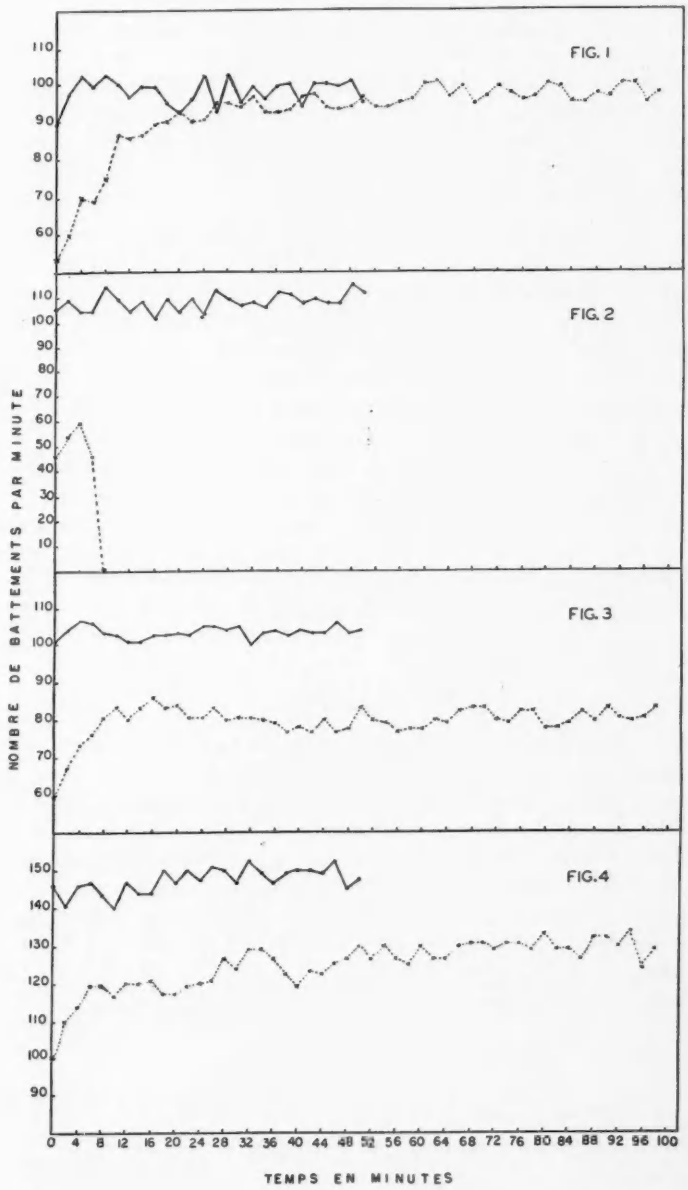
Cette contribution rapporte les résultats que nous avons obtenus après avoir injecté des insectes, (1) avec le véhicule seul (solvant, stabilisateur et diluant); (2) avec une suspension de roténone; (3) avec une suspension de DDT, pour fins de comparaison; puis (4) avec le dérivé cyanuré du DDT.

Protocole expérimental

Tous nos essais furent faits sur des mâles adultes de *Periplaneta americana* (L.) agés de cinq à quinze jours.

L'insecte est fixé sur une planchette de liège. Les élytres et les ailes sont sectionnés à la base. Cette préparation est portée dans le champ d'une loupe binoculaire. La lampe à microscope qui fournit l'éclairage est munie d'un filtre à l'eau afin de refroidir le faisceau lumineux. Le comptage des pulsations cardiaques se fait en observant le cœur à travers le tégument du quatrième ou du cinquième segment abdominal, et à l'aide d'un chronomètre et d'un podomètre.

Étant donné la variation de rythme assez considérable d'un individu à l'autre (86 à 156 contractions par minute) on doit noter au préalable la fréquence des contractions chez chaque insecte qui va être soumis à l'expérience. Nous avons pu observer, cependant, que le rythme chez un individu normal demeure sensiblement régulier en l'absence de stimulus mécanique ou visuel brusque, et pourvu qu'il n'y ait pas de fortes variations de la température. Ces déterminations du rythme cardiaque chez l'insecte normal sont faites à toutes les deux minutes pendant 50 min.



FIGS. 1 to 4. ●———● avant injection; x - - - - - x après injection.

FIG. 1. Véhicule. FIG. 2. Roténone (100 mg./kg.). FIG. 3. DDT (100 mg./kg.). FIG. 4. Dérivé cyanuré (100 mg./kg.).

Le véhicule est le même que celui que nous avons employé dans des études toxicologiques antérieures (1). Ce véhicule, le même pour tous nos essais, consiste en une solution contenant 2000 mg. d'acétone[4] (solvant) par kg. de poids ainsi que 3125 mg. de diéthylène glycol dilaurate[5] (stabilisateur) par kg. de poids. Pour les essais des composés à étudier, le composé chimique est d'abord dissout dans l'acétone; on ajoute le stabilisateur puis finalement de l'eau distillée pour compléter le volume total de la suspension à 10 ml.

Afin de pouvoir injecter l'insecte sans accident, on l'anesthésie au gaz carbonique. Le volume injecté est toujours de 0.03 ml., volume que *Periplaneta americana* peut supporter sans préjudice, ainsi que nous l'avons démontré dans des travaux antérieurs (2). Après injection, la détermination du rythme cardiaque est faite de nouveau, après 15 min. d'attente. Les comptages sont faits à toutes les deux minutes pendant 98 min.

La concentration des substances soumises à l'essai était fixée au taux de 100 mg. de produit par kg. de poids d'insecte. Cette valeur nous a semblé intéressante puisqu'elle était bien au delà, chez les mâles, des doses médianes léthales de chacun des composés essayés, v.g. roténone (2 mg./kg. de poids), DDT (6.2 mg./kg. de poids), dérivé cyanuré (54 mg./kg. de poids) (1). Pour chaque concentration de substance soumise à l'essai, nous avons fait nos expériences sur au moins trois individus différents. Tous nos travaux ont été effectués à la température de la pièce (20° C. à 26° C.); cependant la plus forte variation enregistrée au cours d'une même expérience ne dépassait pas 1° C.

Résultats

Nous avons résumé nos données dans le tableau I. Nous présentons ici la courbe la plus typique de chaque série d'essai (figures 1, 2, 3, 4). La présentation graphique de nos résultats donne la fréquence des pulsations, tout d'abord pour un insecte normal, puis pour le même individu après injection. Les deux courbes sont superposées. Nous avons placé le nombre de pulsations par minute en ordonnées, et le temps (en minute) en abscisses. Le tracé à traits pleins représente le rythme chez l'insecte normal; le pointillé montre la fréquence après injection. Quelques déterminations du rythme cardiaque que nous avons faites chez des insectes ayant été soumis à l'anesthésie au CO_2 nous ont démontré qu'après 15 min. le myocarde a repris son rythme normal. Walling (15) et Walker (14) ont d'ailleurs démontré l'innocuité de l'anesthésie au CO_2 pour l'insecte.

(*A*) *Influence du véhicule*

Lors du début du comptage des contractions cardiaques, 15 min. après l'injection, on remarque (cf. figure 1) un rythme considérablement ralenti. Cependant le myocarde revient graduellement à son rythme normal et cette période de recouvrement ne dure jamais plus que 30 min. Le véhicule n'a

[4] *Acétone U.S.P. de Merck & Co. Ltd.*
[5] *Diéthylène glycol dilaurate technical de Eastman Kodak Co.*

TABLEAU I

VITESSE MOYENNE DES PULSATIONS CARDIAQUES, EN BATTEMENTS PAR MINUTE, CHEZ *Periplaneta americana* L. INJECTÉE AVEC 0.03 ML. DU VÉHICULE ET DE SUSPENSIONS D'INSECTICIDES

Produit injecté	Insecte no.	Avant injection	Minutes après injection		
			0–32	34–66	68–98
Véhicule	1	106	102	111	114
	2	113	88	111	108
	3	99	83	101	94
	4	98	84	96	97
	5	106	99	109	110
	6	130	117	131	131
	Moyenne	109	96	110	109
Roténone	1	108	26m.*		
100 mg./kg. de poids d'insecte	2	130	26m.		
	3	131	A†		
	4	126	42m.		
	5	143	A		
	6	137	30m.		
	Moyenne	129			
DDT	1	103	79	79	81
100 mg./kg. de poids d'insecte	2	104	83	81	81
	3	135	95	100	101
	Moyenne	114	86	87	88
Dérivé cyanuré	1	103	90	108	107
100 mg./kg. de poids d'insecte	2	104	89	96	107
	3	103	92	84	84
	4	97	75	92	93
	5	140	116	127	123
	6	147	119	126	130
	Moyenne	116	97	106	107

* *Le symbole 26m. etc. signifie qu'il y a arrêt des battements du cœur 26 min. etc. après injection.*

† *Le symbole A signifie qu'il y a arrêt des battements du cœur avant le début des comptages c'est-à-dire en deçà de 20 min. après injection.*

pas d'effet durable sur la fréquence des contractions et celle-ci demeure normale jusqu'à la fin des observations, soit pendant plus d'une heure et demie. On remarquera d'ailleurs ce phénomène de désaccélération temporaire, subséquent à l'introduction d'un volume liquide dans l'hémocœle, dans tous nos autres essais.

(*B*) *Influence de la roténone*

L'effet de ce composé sur le rythme cardiaque est très marqué (cf. figure 2). On voit qu'après une tendance vers le rétablissement du rythme normal l'action de la roténone s'établit et provoque une chute rapide de la fréquence jusqu'à ce que le myocarde s'arrête en diastole.

Ces résultats s'accordent avec ceux de Tischler (12) qui avait noté, chez la larve de *Bombyx*, un ralentissement du rythme cardiaque subséquent à

l'application externe de poudre de Derris. De même, Krijgsman *et al.* (7) ont observé ce même phénomène après application de roténone directement sur le cœur de *Periplaneta americana*. Plus récemment, Orser et Brown (11) ont obtenu des résultats identiques après injection de roténone dans l'hémocœle du même insecte.

(*C*) *Influence du 1,1,1-trichloro-2,2-bis-(p-chlorophényl)-éthane*

Avec ce composé, la chute caractéristique qui suit l'injection est suivie à son tour d'un rétablissement partiel du rythme cardiaque jusqu'à un niveau légèrement inférieur au normal (cf. figure 3).

(*D*) *Influence du 1,1,1-trichloro-2,2-bis-(p-cyanophényl)-éthane*

On remarque, dans la figure 4, la chute caractéristique de la fréquence des contractions, suivie d'une accélération graduelle jusqu'à un niveau à peu près constant. Ce niveau est atteint environ trente minutes après le début des observations. Cependant, après l'injection du composé cyanuré, comme nous l'avons remarqué d'ailleurs pour le DDT, ce niveau ne retourne pas à la normale, mais il demeure légèrement inférieur pendant toute la durée des observations.

Discussion et Conclusion

Nous avons observé, au cours de nos travaux, que le dérivé cyanuré montre une action analogue à celle du DDT, quant aux symptômes généraux d'intoxication. Il en est de même pour son action sur le cœur de *Periplaneta americana*. Davenport (5) a lui aussi constaté que le cœur isolé de l'orthoptère, *Stenopelmatus longispina* Brunner, baignant dans une suspension de DDT, continue à se contracter pendant plusieurs heures mais à un rythme légèrement ralenti; que les contractions se continuent à une fréquence sensiblement régulière, sauf pendant les spasmes violents qui saisissent la musculature abdominale.

Par ailleurs Orser et Brown (11) rapportent que le DDT, injecté en solution dans l'hémocœle de *Periplaneta americana*, n'aurait que peu ou pas d'effet sur le rythme cardiaque, ou bien, s'il en a, c'est un effet légèrement accélérateur. Ces auteurs ajoutent, cependant, que la variabilité de leur matériel biologique est telle qu'ils ne peuvent conclure à une action accélératrice.

Nous avons vu (4, 6, 10, et 3) que ni l'intégrité ni même la présence d'un appareil nerveux associé au cœur ne sont essentiels à la contraction cardiaque de certains insectes. Le "pacemaker" du mécanisme cardiaque chez l'insecte pourrait donc être myogénique.

Les observations de Duwez (6) sur le cœur isolé du dytique, i.e. sur un cœur qui n'est plus soumis aux influences nerveuses, ressemblent bien à celles de Davenport (5), sur *Stenopelmatus longispina* soumise à l'influence du DDT, et aux nôtres sur *Periplaneta americana*, soumise à l'influence du DDT et

de son dérivé cyanuré. Le "pacemaker" myogénique de l'insecte pourrait donc être soumis à une influence accélératrice neurogénique.

Tobias, Kollros et Savit (13) ont démontré que le DDT provoque une augmentation considérable de l'acétylcholine dans le système nerveux de l'insecte, sans affecter l'activité de la cholinestérase. Si, comme le proposent Krijgsman *et al.* (8), le mécanisme cardiaque de l'insecte possède un appareil de contrôle cholinergique avec transmission synaptique, le DDT devrait avoir une influence indirectement accélératrice sur le rythme cardiaque, ce qui, nous l'avons vu, n'est pas le cas.

Remerciements

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TWO NEW SPECIES OF DERMATITIS PRODUCING SCHISTOSOME CERCARIAE FROM CULTUS LAKE, BRITISH COLUMBIA[1]

By D. K. Edwards[2] and Marjorie E. Jansch

Abstract

Two new schistosome cercariae capable of producing a dermatitis are described; *Cercaria columbiensis*, n.sp. and the cercaria of *Trichobilharzia adamsi*, n.sp. A female adult of *T. adamsi* n.sp. is also described.

Introduction

A severe outbreak of schistosome dermatitis occurred at Cultus Lake in 1950. As a result a Dominion Public Health Research Grant was made available to the Department of Zoology, University of British Columbia, for the investigation of schistosome dermatitis in this province. Research, under the direction of Dr. J. R. Adams, was instituted by Mr. S. M. Sager and Miss M. Thom in 1951 and continued by the present authors in 1952 and 1953.

In the summer of 1953, two new species of schistosome cercariae were discovered at Cultus Lake. Both emerged from *Physa* c.f. *coniformis* Tyron. They are described herein together with the adult form of one of them that was obtained following experimental infection. The adult is described under the name *Trichobilharzia adamsi* and the name *Cercaria columbiensis* is proposed for the other cercaria.

Methods and Apparatus

Methods of Study of the Larval Forms

All cercariae were obtained from snails collected within a restricted area at Cultus Lake, B.C. This area is located along the northwest shore line between Mallard Point and Redtail Creek. In the laboratory the snails were kept in quart jars and were fed upon pieces of "chick-weed" (*Stellaria* sp.). Its leaves did not decompose as fast as those of lettuce. Cercarial emergence was induced by changing the water in the jar, as reported with regard to *Cercaria ocellata* (1), or stimulated by shining a beam of light through the jar (5). An accurate emergence time was not obtained.

Methods Used in Life Cycle Studies

Initial life cycle investigations were begun during the fall of 1952 and the spring of 1953 by trapping small mammals near the region in which infected snails had been collected. Mouse traps were baited with walnuts. Animals caught were examined by direct observation of the mesenteries and

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liver and by utilization of the side-arm flask technique (2). During the summer of 1953 a few more small mammals were caught by the same method. Attempts were made in the laboratory to induce the cercariae to penetrate into white mice. Olivier and Stirewalt (6) outlined a system for restraining mice while subjecting them to penetration of cercariae through the tail. However, use of this techinque in the present study was hindered by a lack of sufficient numbers of cercariae. A method was therefore sought which would increase the concentration of the cercariae in the exposed region of the mouse and which would also restrain the movements of the animal. This was accomplished by putting the infected snails into a McMullen and Beaver (2) side-arm flask which was filled with water so that the level in the arm was higher than that in the neck, the latter reaching only to the opening of the arm. The flask was then covered in the usual manner, leaving the arm exposed. With a strong light shining through the arm, cercariae soon became concentrated there in large numbers. A mouse was fixed in a specially prepared clamp above the side-arm with the tail immersed in the arm. By taking advantage of the different cercarial taxes one may make admirable use of this technique in separating double infections.

For exposure to the cercariae Peking ducklings ranging in age from one week to one month were allowed to stand in water approximately one inch in depth containing the trematodes. Cercariae were also applied to the inguinal region of a guinea pig and a few were administered orally.

The adult of *Trichobilharzia adamsi* was initially suspected of being a parasite of birds on the basis of the flame cell pattern and general morphology of the cercaria. Experimental attempts were made to raise adult worms in two Peking ducklings (*Anser domesticus*) aged approximately one month. One duck was sacrificed 42 days after exposure to cercariae. The viscera were examined with a dissecting microscope and by comminution of the liver in citrated saline. The remaining duck was allowed to live for an additional 28 days to allow any worm which might be present to mature.

Faecal checks of animals previously subjected to cercariae were made at intervals. The animals were later killed with intraperitoneal nembutal and were examined for adult schistosomes. The livers of the mice were perfused using a modification of the Yolles technique (10), while the intestinal blood vessels and mesenteries were examined with a dissecting microscope. Viscera of the ducks and guinea pig were examined under a dissecting microscope and the duck livers were comminuted in citrated saline.

Results

Trapping yielded 39 *Peromyscus* spp., 2 *Microtus* spp., and 13 *Sorex* spp. In addition one mink was caught with a larger trap. Examination revealed no schistosomes in these animals.

All laboratory animals were found to be negative except one duckling which had been exposed to the cercariae of *Trichobilharzia adamsi*.

Cercaria columbiensis n. sp. (Figs. 1, 2, and 3)

This cercaria is an apharygneal distome cercaria of the "spindalis group" and closely resembles the cercaria of *Gigantobilharzia huronensis* Najim 1950. Measurements were made of 25 specimens fixed in 15% hot formalin. The means are given with the standard error: body length 0.1985 ± 0.0094 mm.; body width 0.0779 ± 0.002 mm.; tail stem length 0.2092 ± 0.0045 mm.; tail stem width, proximal 0.0366 ± 0.0014 mm., distal 0.0260 ± 0.0006 mm.; furcal length 0.096 ± 0.0049 mm.; furcal papilla length 0.0120 ± 0.0003 mm.; oral sucker width 0.0537 ± 0.0011 mm.; ventral sucker 0.0295 ± 0.006 mm. by 0.0216 ± 0.0082 mm.

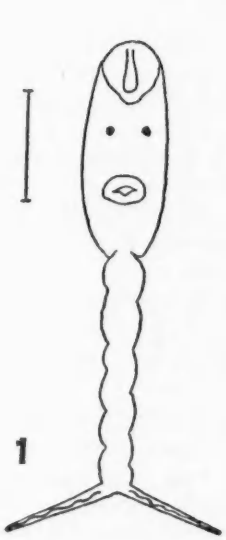
The tail stem is slightly longer than the body and is contractile. The tail stem cuticle is characteristically thrown into many prominent indentations when the tail is contracted (Fig. 1). Furcal finfolds are present.

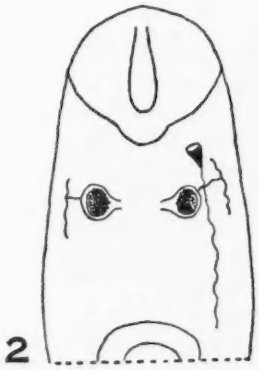
The entire body, tail stem, and furcae are covered with small retrorse spines, those of the body being of uniform small size. The spines of the tail stem and furcae are spaced farther apart than those of the body and are heavier in structure. Pairs of papillar spines are present on the lateral aspects of the body (Fig. 3). One pair is on the oral sucker about midway between the most anterior point of the oral organ and the junction of the oral organ with the lateral body cuticle. Two pairs are located close together immediately posterior to the above junction. Another pair is present just anterior and lateral to the eyespots. Finally, papillar spines are seen laterally near the ventral sucker. These spines are more readily seen than those of the cercaria of *T. adamsi.*

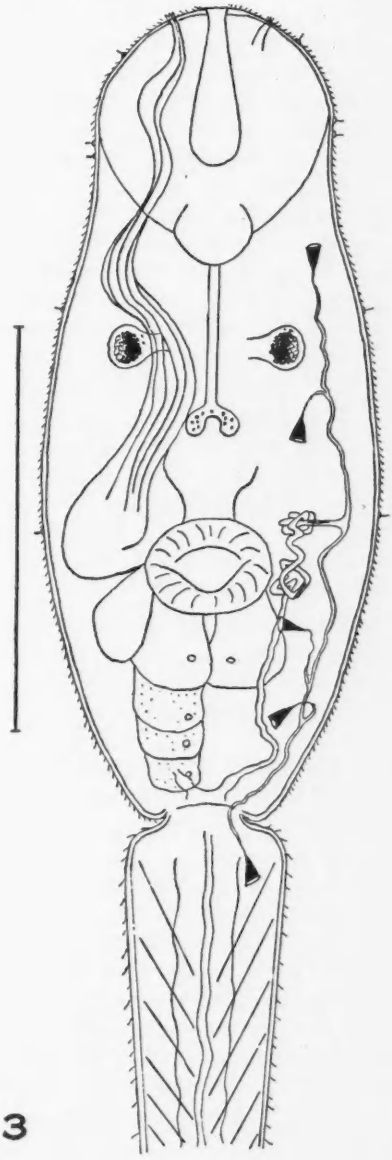
The eyespots of this cercaria are composed of dark brown granules which tend to be scattered. There is a lateral "lens". A fine ring surrounds each eyespot and extends toward the mid-line. Leading laterally from each ring and crossing the anterior collecting tubule of the excretory system is a very fine linear structure which may be a nerve tract (Fig. 2). This bifurcates laterally into an anterior and posterior "line".

The digestive tract consists of a long, fine esophagus, bifurcating midway between the level of the eyespots and ventral sucker to form two short, club-shaped caeca containing central acidophilic granules which stain with neutral red.

Of the five pairs of penetration glands, the anterior pair are deeply divided into either two or three lobes. The anterior two pairs of penetration glands surround the ventral sucker and contain clear and brightly refractile cytoplasm. The posterior three pairs of gland cells are smaller, lie in a linear fashion behind the ventral sucker, and are more coarsely granular. The ducts of the penetration glands follow a somewhat tortuous course to pass into the oral organ. They terminate at five pairs of papillae which can be retracted to well within the oral organ or extended to the most anterior portion of the body.







In all figures the straight line represents 0.1 mm.

FIG. 1. *Cercaria columbiensis*, showing wrinkled tail stem.

FIG. 2. *C. columbiensis*, showing circumocular rings and structures which may be nerve tracts.

FIG. 3. *C. columbiensis*, dorsoventral view illustrating morphology. The excretory system is shown on one side only, with penetration glands shown only on opposite side for clarity.

The excretory system consists of five pairs of flame cells, four pairs within the body and one pair in the anterior portion of the tail stem. In the body two pairs of flame cells lead into the anterior collecting tubule and two pairs lead into the posterior collecting tubule. Thus, the flame cell pattern may be expressed as $2(2 + (2 + 1)) = 10$. Two distinct convoluted regions occur in the main collecting tubules near the origin of their anterior and posterior branches. Two ciliated patches are present in the same area, one near the bifurcation of the main collecting tubule and one within the coils of the more posterior convolution. The main collecting tubules run posteriorly where they join the vesicle whose outline was not clearly defined. No Island of Cort was seen in the bladder. The central excretory tubule passes from the vesicle down the center of the tail stem, bifurcates anterior to the furcal bases, and a branch runs through each furca to open through a long terminal papilla at the furcal tip.

Cercaria columbiensis is markedly negatively geotactic, tending to cling to the surface film by the ventral sucker. It is usually necessary to view the surface of the water to appreciate the numbers within the vial. The cercariae are positively phototactic and light may alter the geotaxis to some extent. The cercaria tends to lose its tail easily but its body remains viable for long periods under a coverslip. Under a coverslip the cercaria hitches along by gripping alternately with its oral and ventral suckers.

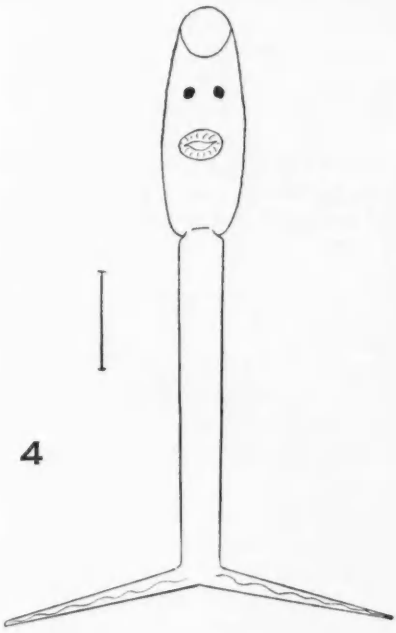
Although attempts were made to infect laboratory animals with *Cercaria columbiensis* these were unsuccessful. Since Najim (3) found *Gigantobilharzia huronensis*, a similar form, in goldfinches, further life cycle studies using passeriform birds might be more successful in discovering a definitive host.

Trichobilharzia adamsi n.sp.

Cercaria (Figs. 4, 5, and 6)

The cercaria of *Trichobilharzia adamsi* is an apharyngeal, furcocercous distome and resembles very closely the cercariae of the "ocellata group". Measurements were made of 25 specimens fixed in 15% hot formalin. The means are given with the standard error: body length 0.2301 ± 0.0069 mm.; body width 0.0802 ± 0.0014 mm.; tail stem length 0.3413 ± 0.0023 mm.; tail stem width, proximal 0.0438 ± 0.0008 mm., distal 0.0371 ± 0.002 mm.; furcal length 0.2007 ± 0.0054 mm.; furcal papilla length 0.0173 ± 0.0008 mm.; oral sucker width 0.0515 ± 0.0007 mm.; ventral sucker diameter (for 20 specimens) 0.0372 ± 0.0006 mm.; distance from center of ventral sucker to posterior end of body 0.0966 ± 0.059 mm.

The tail stem is slightly longer than the body (Fig. 4). Dorsoventral fin folds are present on the furcae. The entire body, tail stem, and furcae are covered with minute retrorse spines. The body spines are most obvious on the anterior half and they seem to diminish in size toward the more posterior region of the body. Spines on the tail stem and furcae are spaced farther apart and appear more coarse and sturdy.



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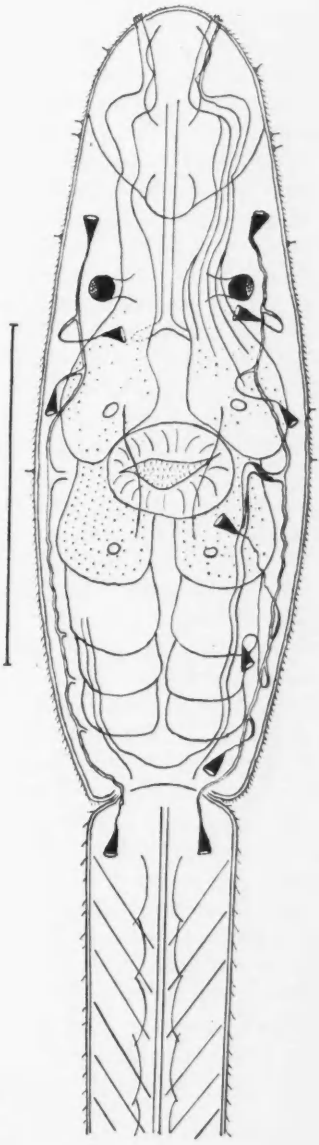

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In all figures the straight line represents 0.1 mm.

FIG. 4. The cercaria of *Trichobilharzia adamsi*, showing proportions.

FIG. 5. Cercaria of *T. adamsi* with body twisted to side to show details of excretory system.

FIG. 6. Cercaria of *T. adamsi*, dorsoventral view illustrating morphology.

Papillar spines are present on the body cuticle. On each side, a spine is located about midway between the most anterior point of the body and the junction of the oral organ with the body cuticle laterally; two are located fairly close together immediately posterior to the above junction; one is situated slightly anterior to the level of the eyespot. Some papillar spines are observed at the level of the ventral sucker and these were less distinct than those farther anterior. In some instances the minute hair located on the papilla nearest the eyespot and on the two papillae near junction of the oral organ and lateral cuticle were very long and distinct. The papillar spines are not all in the same plane of focus.

Two heavily pigmented eyespots are present on the cercaria of *T. adamsi* and these possess a "lens" which is directed laterally. The body contains five pairs of penetration glands, the two anterior pair being more granular in appearance than those more posterior. The glands are arranged as illustrated in Fig. 6. An esophagus was observed beginning within the oral sucker and running posteriorly between the penetration gland ducts to terminate with a bifurcation into two short caeca.

The excretory system consists of six pairs of flame cells within the body and one pair in the tail stem, all leading through a system of collecting tubules into an excretory bladder. The flame cells are situated as illustrated in Figs. 5 and 6 and the excretory formula is therefore $2(3 + (3 + 1)) = 14$. In one cercaria the flame cell normally located immediately posterior to the eyespot was seen to be adjacent to the flame cell number one and its junction with the anterior tubule was also anterior to the eyespot. This situation existed on one side of the cercaria only. Najim (3) observed similar anomalies in the excretory system of the cercaria of *Gigantobilharzia huronensis*. In the cercaria of *T. adamsi* two ciliated patches are located near the bifurcation of the main collecting tubule on each side of the body. The outline of the excretory bladder was very obscure. No Island of Cort was observed.

The cercaria of *T. adamsi* is positively phototactic. Some of the cercariae attach by the ventral sucker to the side of the glass nearest to the light, where they form a U shape. The cercariae did not congregate at the surface film. When resting the furcae are usually held together. Under a coverglass the cercariae are rarely observed lying in a dorsoventral position because of the degree of protrusion of the ventral sucker. They sometimes hitch along under a coverglass by alternate attachment of the ventral and oral suckers.

The cercariae emerged from a single snail, *Physa* c.f. *coniformis*. Twenty-five *Physa* were taken from the collecting area at Cultus Lake on August 3, 1953, and of these only one was infected with cercariae of *T. adamsi*.

Adult Female Worm (Fig. 7)

One immature adult female schistosome was found in the liver sediment of the duckling sacrificed 42 days after exposure to cercariae. The worm was considered immature since no eggs were present within the uterus and previous faecal examinations had not revealed ova. No ova were found in faecal

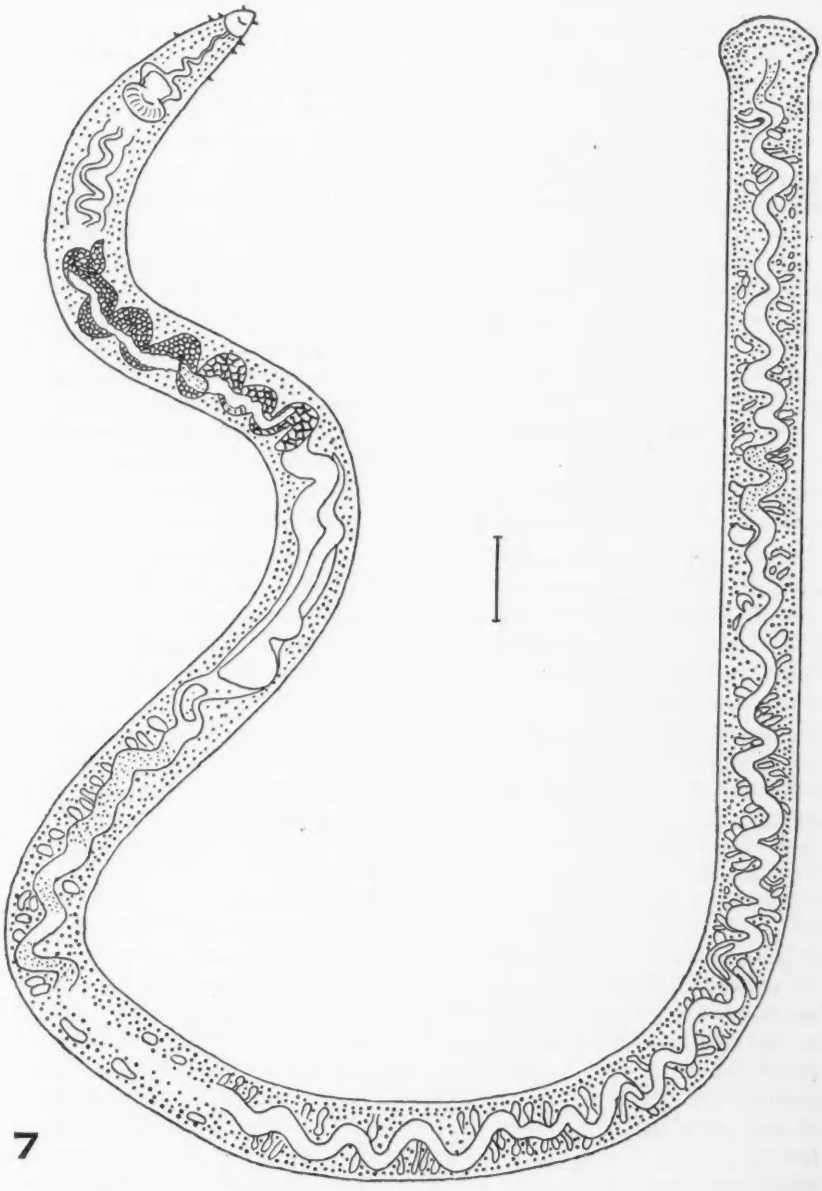

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FIG. 7. *Trichobilharzia adamsi;* immature adult female.
The straight line represents 0.1 mm.

checks and dissection of the second duck did not reveal schistosomes. The single worm found was studied while living. It was then examined after it had been killed with formalin and was examined finally from a permanent mount. For mounting it was stained with acetic-alum-carmine and counter-stained with light green.

The worm was discovered in the liver residue one-half to three-quarters of an hour after the liver had been removed from the duck. At this time the worm was quite active. Since, when brought beneath a coverglass, it did not at any time stretch out into a straight line, measurements of the body length were very difficult to obtain. Measurements obtained from the worm are given as follows. The bracketed statements refer to the condition of the worm under which the individual measurements were obtained: body length 3.61 mm. (in 15% formalin); body width across ventral sucker 0.105 mm., farther posterior 0.093 mm. (*in vivo*); ventral sucker width 0.064 mm., length 0.026 mm. (in 15% formalin); oral sucker width 0.036 mm., length 0.039 mm. (in 15% formalin); lateral cuticle thickness 0.004 mm. (in 15% formalin); ventral sucker to oral sucker 0.111 mm. (permanent mount); ventral sucker to esophageal bifurcation 0.026 mm. (permanent mount); ovary to back of ventral sucker 0.175 mm. (permanent mount).

The entire body of the adult is distinctly flattened, especially the posterior half. The posterior end is truncate and consists of three lobes, two lateral and one median. Coarse spines cover the anterior portion of the body. These are arranged in lines running transversely over the cuticular surface. Spines between the ventral sucker and more posterior regions of the body are more difficult to observe than those at the anterior and posterior ends. Minute papillar spines, observed only "*in vivo*", are located on the lateral cuticle near the extreme anterior end of the worm. Three bilaterally disposed pairs were observed and these were situated as illustrated in Fig. 7. Another spine was observed farther posterior on one side of the body and it is probable that another existed opposite this on the other side. Thus, not only are these papillar spines carried through from the cercaria to the adult, but the relative positions of the more anterior spines of the cercaria are also retained in the adult. The ventral sucker is at first observed only with difficulty. It possesses an almost globular appearance. Long, radially arranged spines are present on the convex surface of the organ. A narrow, somewhat twisted esophagus leads from the oral sucker posteriorly to a level slightly anterior to the ventral sucker. At this point the esophagus bifurcates forming two pouch-like structures laterally and immediately anterior to the ventral sucker. The two caeca then approach the mid-line and disappear in the region of the ventral sucker. The posterior portion of the esophagus and especially the two lateral pouches of the caeca contained masses of yellow granules which may have been remains of erythrocytes. Between the ventral sucker and the posterior end of the ovary the course of the caeca was not observed and their position is uncertain. Posterior to the ovary the intestine undulates as a single unbranched tube to a point within the flattened truncate end.

It could not be determined whether the lateral caeca anterior to the ventral sucker again unite in the immediate vicinity of the sucker or whether this union occurs farther posteriorly in the region of the ovary. This latter condition exists in the closely similar forms, *T. ocellata*, *T. stagnicolae*, and *T. physellae* (McMullen and Beaver (2)). The manner in which the two lateral pouch-like enlargements anterior to the ventral sucker approach the mid-line seems to suggest in its very abruptness a fusion of these tubes in the immediate vicinity of the ventral sucker. The question must for the moment remain an open one.

The fairly conspicuous ovary is slightly convoluted possessing four and one half loops along its length. No trace could be seen of the rest of the reproductive system. A vitelline duct was observed superimposed upon the surface of the ovary and extending farther posteriorly along the intestinal tract. The anterior and posterior terminations of this duct were indistinct. Numerous vitellaria are scattered farther posteriorly on either side of the intestinal tract and these continue to a point slightly anterior to the beginning of the posterior lobation of the body.

The worm possessed clusters of yellow, glistening globules in the portion of the body anterior to the ovary. They were most concentrated in the region anterior to the ventral sucker.

Discussion

A comparison will be made chiefly between schistosomes which go through physid snails, are dermatitis producers, and in which the cercariae possess either six or four pairs of body flame cells. The cercaria of *Trichobilharzia adamsi* is a member of the "ocellata group" of Sewell. There is some superficial resemblance of this cercaria to *Cercaria oregonensis* MacFarlane and Macy 1946, but specific differences in measurements exist. Further, there are differences in the position of the penetration glands of the cercariae and also in the excretory system.

TABLE I

COMPARISON OF MEASUREMENTS OF THE CERCARIA OF *T. adamsi* AND *Cercaria physellae*

Dimension	Cercaria of *T. adamsi*, in mm.	*C. physellae*, in mm.
Body length	0.2301 ± 0.0069	0.265 ± 0.0084
Body width	0.0802 ± 0.0014	0.060 ± 0.0046
Tail stem length	0.3413 ± 0.0023	0.374 ± 0.0106
Tail stem width	0.0438 ± 0.0008	0.040 ± 0.0036
Furcal length	0.2007 ± 0.0054	0.196 ± 0.0078
Oral sucker diam.	0.0515 ± 0.0007	0.039 ± 0.0020
Ventral sucker diam.	0.0372 ± 0.0006	0.029 ± 0.0024

The cercaria of *Trichobilharzia cameroni* Wu (9) closely resembles that of *T. adamsi*. However, a significant difference exists between the two forms in the ratio of the body length to the tail stem length. The most obvious points of difference between these two species are seen upon comparison of the adults. The cercaria of *T. szidati* (4) is dissimilar to that of *T. adamsi* in that the host is a lymnaeid and that its general body measurements are less. However, Neuhaus (4) describes a papillar type of spination like that of the cercaria of *T. adamsi*.

The adult female *T. adamsi* resembles most closely *T. physellae*. *T. adamsi* is considerably wider than the latter especially in the region near the ventral sucker and this difference is reflected in the width of the ventral suckers. The body thickness of *T. physellae* is between one-half and two-thirds that of the width. Measurements of the permanent mount of *T. adamsi* indicated that the thickness is about two-fifths of the width immediately posterior to the ventral sucker. It is doubtful that the condition of *T. adamsi* as a permanent mount would be responsible for this difference in width. McMullen and Beaver (2) indicated that in some cases *T. physellae* appeared to possess extremely fine spines which were especially obvious near the middle of the body of the male. The body spines of *T. adamsi* are readily seen and are especially obvious anterior to the ventral sucker.

The width of *T. cameroni* is described as being from 0.052 to 0.059 mm. in the region of the ovary. This compares unfavorably with the width of *T. adamsi*. The ventral sucker of *T. adamsi* is not as prominent as that described by Wu. Further, *T. cameroni* possesses no body spination.

Other species of *Trichobilharzia* go through snail hosts of families other than the Physidae. Some further differences are given as follows. *T. ocellata* (2) differs from *T. adamsi* in the dimensions of the oral sucker, the distance between the acetabulum and esophageal bifurcation, and in other measurements at the anterior end. *T. stagnicolae* (2) was described as being at least 5.4 mm. in length and 0.032 mm. wide across the ovary. Further, the esophageal bifurcation is 0.068 mm. anterior to the ventral sucker as compared with 0.026 mm. in *T. adamsi*. *T. szidati* (4) is in many respects similar to *T. adamsi*, e.g., the fine body spination, however, no papillar spines are noted in *T. szidati*. *T. szidati* female adult measurements indicate that it is shorter in length than *T. adamsi;* its length being 3.00 mm. as opposed to 3.61 mm. Its width is also less than that of *T. adamsi*; maximum width being 0.036 mm., minimum width being 0.020 mm. It is thus unlikely that these two species could be considered similar.

Papillar spines have not been described on any known adults of *Trichobilharzia* and, as far as can be determined, on any adult schistosomes. In addition, none seem to have been observed possessing yellow globules as described herein.

In the past, only two dermatitis producing cercariae have been described which possess an excretory system consisting of four pairs of flame cells in

the body. These are the cercaria of *Schistosoma spindalis* Montgomery 1906 (7), and the cercaria of *Gigantobilharzia huronensis* Najim 1950 (3). The former was found in Malaya while the latter has been reported from Michigan. The cercaria of *S. spindalis* is similar macroscopically to *Cercaria columbiensis*. However, the former possesses no eyespots and the distribution of the penetration glands of the two cercariae differs.

The cercaria of *G. huronensis* resembles *Cercaria columbiensis* very closely in all respects and the two may in future be found to be synonymous. The similarities between the two cercariae include swimming behavior, body proportions, possession of papillar spines, number of penetration glands, and granulation of these glands. According to Najim variations in the morphology of the excretory system were frequently noticed in his cercaria. In the author's own words, "variations in the position of the flame cells and the looping of the tubules were noticed quite often". The *number* of flame cells were even found to vary, an "extra" one being noted at times posterior to the ventral sucker. It is possible that a ciliated patch was mistaken for a flame cell in this latter case, but it seems equally possible that the cercaria possessed a greater number of flame cells than were described by Najim. This author also mentions that the third and fourth flame cells "might come closer together in position". In view of this apparently high degree of variation in the excretory system it is possible that the cercaria of *G. huronensis* possesses more than four pairs of body flame cells.

The cercaria of *G. huronensis* differs from *C. columbiensis* in possessing a large, presumably neural structure immediately anterior to the ventral sucker. Nothing comparable to this in size was observed on *C. columbiensis*. In addition, Najim's cercaria is described with the second pair of glands lobed, while the first pair of glands of *C. columbiensis* are lobed. Nothing more concerning the possible synonymity of these two cercariae should be said until the adult of *C. columbiensis* has been described. *C. columbiensis* has been described as a new species pending discovery of the adult.

In 1953 the cercaria of *T. adamsi* and *C. columbiensis* were found within the small restricted area at Cultus Lake already described. Other cercariae were obtained from adjacent areas and from regions farther removed, but the two trematodes described herein were never found with them during that year. *C. columbiensis* was obtained from snails collected on July 4 and July 29. Later in the summer, on Aug. 3, cercariae of *T. adamsi* were obtained from one snail collected in the same area and *C. columbiensis* was no longer present. Cercariae of *T. adamsi* were also obtained during June, 1954, from another area far removed from the former. Since the definitive host of *T. adamsi* was experimentally determined to be a domestic duck, it is reasonable to suspect that water fowl are the natural hosts at Cultus Lake. Large numbers of these have been observed during the day far out toward the middle of the lake and it is likely that water fowl visit the collecting area occasionally.

The nature of the definitive host of *C. columbiensis* has not been determined and therefore little can be said concerning the ecological factors affecting

the cercarial distribution. Since this cercaria closely resembles that of *Gigantobilharzia huronensis* which matures in goldfinches and cardinals, the Cultus Lake cercaria may mature in passeriform birds. Goldfinches are found along the shore in the vicinity of the collecting area.

Chronological Factors

Examination of the shells of the 1953 snails from which cercariae escaped revealed that the molluscs presumably had hatched during that same year. These snails could not have been infected in the fall of the previous year thus carrying the infection over the winter. However, recent findings have revealed that in some cases the trematodes may spend at least a part of the winter in the intermediate host. Five large, mature adult snails from the 1953 crop have recently been discovered and these, which had wintered over in the lake, were infected with *T. adamsi.* This may result in two overlapping periods of emergence during the summer.

Acknowledgments

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DISEASE AS A CONTROL OF A POPULATION OF BLUE GROUSE, *DENDRAGAPUS OBSCURUS FULIGINOSUS* (RIDGWAY)[1]

By J. F. Bendell[2]

Abstract

A population of blue grouse was studied on its summer range at Quinsam Lake, Vancouver Island, to determine the factors of importance in population control. The population is stable with a density of 0.40 adult males and 0.78 yearling and adult females to the acre. A life table is constructed on the basis of a stable population, the death of 80% of the chicks in the first three months after hatch, and the death of 31% of the adults each year, as calculated from banding returns. The survivorship curve is negatively "J"-shaped. Mortality rates appear constant and independent of age after the first year of life. Space, weather, food, predators, and disease are considered as factors capable of population control. Six parasites are new records in this host. Two of the six, *Plagiorhynchus formosus* and *Dispharynx nasuta* occur commonly and almost exclusively in the chicks, where they cause extreme damage to the tissues of the gut. It is concluded that parasitism by these helminths is an important mortality factor in the chicks and a major cause of population stability—an equilibrium between death in the older age classes and replacement by surviving young.

Introduction

The growth rate of an animal population is a function of its birth rate, death rate, and rate of dispersal into and out of the space which it occupies. These phenomena can be considered as the result of the environmental factors: weather, space, food, predators, and disease.

Accordingly it becomes a problem to the student of population dynamics to find whether a particular animal population is stable, increasing or decreasing, and then to explain how the environmental factors are affecting the death rate, birth rate, and dispersal of the animal to produce this observed rate of population growth. This is attempted in a consideration of the population dynamics of the blue grouse at Quinsam Lake.

Data on the life history of the blue grouse have been reviewed and augmented by Fowle (12) and further information added to the literature by Beer (2, 3), Wing (21, 22), Wing *et al.* (23), Schottelius (18), and Bendell (4, 5, 6). A most striking feature of the bird is its altitudinal migration. In spring the breeding birds descend from the fir forests of the mountains, where they winter, to the open lowlands. Here they breed. In August the males return to the timbered slopes followed by the females and young in late August and September.

[1] *Manuscript received January 11, 1955.*

Contribution from the Department of Zoology, University of British Columbia, Vancouver, B.C. Part of a doctoral thesis submitted to the Department of Zoology, University of British Columbia, 1954. The work was supported by N.R.C. grants-in-aid and R.C.O. scholarships.

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Time and Place of Study

The study was carried out over four years on the breeding range near Quinsam Lake, Vancouver Island. Field work began in June of 1950 and ended late in August. In May of 1951 the study was resumed and continued throughout the summer until the first week in August. Field work began again in April 1952 and as in the previous year terminated early in August. In 1953 the study area was visited in June and July to provide additional data on the return of banded birds and obtain an estimate of the size of population in that year. During intervening periods, data were analyzed in the Department of Zoology at the University of British Columbia and in 1952 at Queen's University, Kingston, Ont.

The study area is part of an undulating coast plain which slopes east from a height of 600 ft. to sea level at the straits of Georgia. To the west and southwest the land continues to rise into the island mountain ranges. An area of approximately four square miles was cruised in banding and collecting grouse, while more detailed work was carried out in two study plots each 36 acres in size.

According to British Columbia Forest Service Records, the study area prior to 1925 was mature forest of douglas fir (*Pseudostuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.)) Sarg., and western red cedar (*Thuja plicata* Donn). As such, it must have been unsuitable breeding range for blue grouse. After 1925, like much of the east coast of Vancouver Island, the Quinsam area was rapidly logged and in the process burned. There are records of logging and burning in the study area in 1927 and 1929. Finally in 1938, a severe forest fire swept 74,500 acres of logged and mature timber from Menzies Bay in the north, thence in a swath two miles in width to Courtenay in the south. The present stage of burn succession is characterized by bare soil, charred logs and stumps, and loose to dense associations of willow (*Salix* spp.) and alder (*Alnus oregona* Nutt.). The most abundant herbs and shrubs are: bracken (*Pteris aquilina* L.), blackberry (*Rubus macropetalus* Dougl.), salal (*Gaultheria Shallon* Pursh), and hare's ear (*Hypochaeris radicata* L.). It is noteworthy that these plants, with the exception of alder, are used in some form as food by the chicks and breeding birds (Fowle (12)).

The Density and Growth Rate of the Population

The two study plots were censused repeatedly in the spring of each year to determine the number of adult males (birds two years of age and older (6)) and adult and yearling females resident on them. The comparison of densities recorded in each year provided a measure of the growth rate or trend in numbers of this segment of the population. The census of sexually active adult males was simplified by their marked territorial behavior (Bendell (4)). Also, most of the males holding territory on the plots were banded or marked in a manner that permitted easy identification. A count of the territories on the two study plots coupled with the number of marked

birds known to be present yielded an absolute and relatively accurate census of the sexually active adult males.

A count of the hens resident in the study plots was more difficult to obtain because the movements of hens are relatively wide as compared to the movements of territorial males. However, the hens are localized and their movements are restricted most before the time of hatch. As with the males an attempt was made to mark all hens observed on or near the study plots. Then assuming that the presence of a hen on a plot was an indication of residence there, a count of marked hens was made on one of the plots prior to hatching time. The figure obtained is supported by an estimate made in the same period by means of the Lincoln index (Lincoln (15)). The Lincoln index seemed applicable in the case of the hens as some were marked and as other experimental conditions were fulfilled (Ricker (17)). The census techniques were used in estimating the absolute number of hens within the boundaries of one plot.

Two census methods were used to provide data on the relative abundance of grouse in each year. The comparison of relative abundance from season to season and year to year provided seasonal and yearly trends of abundance of grouse in the study area. One method was based upon the number of birds observed per hour per week in the entire study area. Census hours were daylight periods between 0800 and 2000 standard time. In this time activity of grouse is relatively uniform (Bendell (5)). The author tallied separately males, females, and females with brood, then divided the total number observed per week by the number of hours spent in the field for that week. The second method of estimating relative abundance applied to incubating hens and was based on the number of clocker droppings found in the study area. All clocker droppings were tallied and the total for each year was divided by the number of hours spent in the field in each year after the first dropping was found. The results of the censuses are presented in Tables I and II, Fig. 1 (*a*, *b*, and *c*), and Table III.

TABLE I

NUMBER OF SEXUALLY ACTIVE ADULT MALES

Plot	1951	1952	1953
I	14	12	12
II	16	18	14
Total	30	30	26

The differences between the total numbers of sexually active adult males on the two study plots over the three years are not statistically significant. By averaging the totals and dividing by 72 the acreage of the two study plots, the figure of 0.40 males per acre is obtained. Considering that this is the density of breeding adult males, this density is extremely high for a gallinaceous bird.

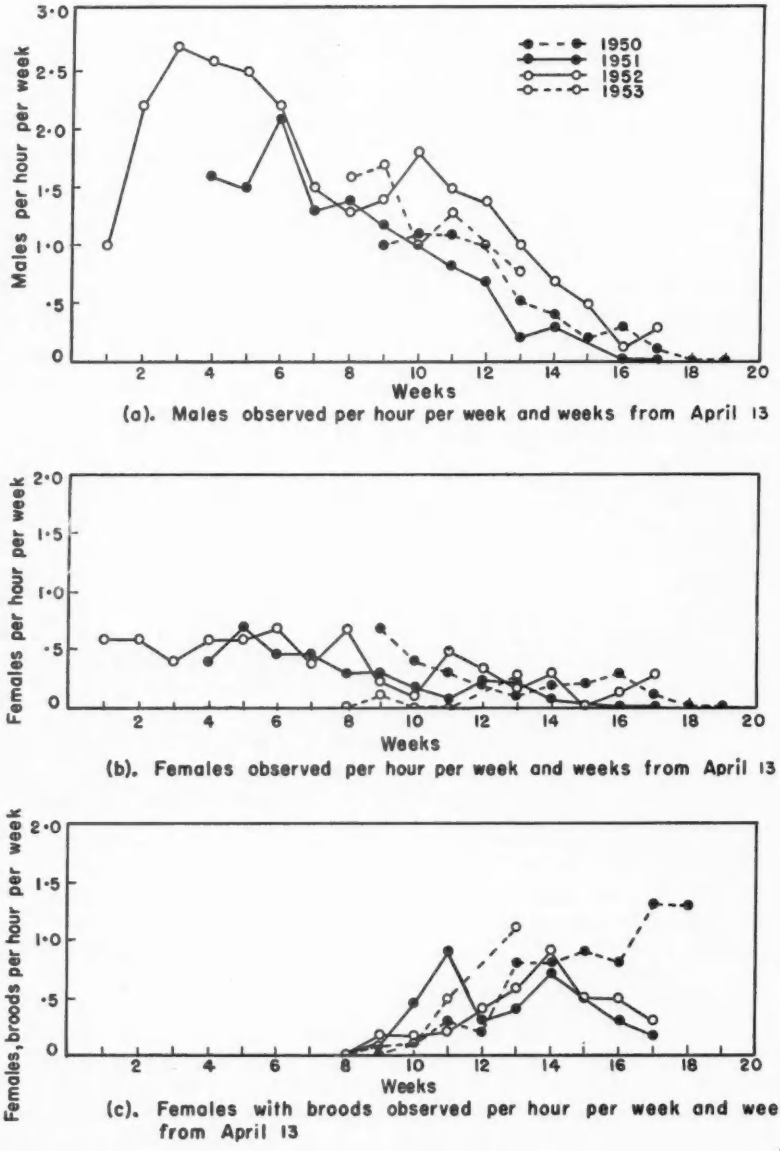

FIG. 1. Number of blue grouse observed per hour per week in the field for 1950, 1951, 1952, and 1953.

TABLE II

NUMBER OF HENS ON PLOT II PRIOR TO HATCH

	1951	1952
Actual count, marked hens	20	22
Lincoln index estimate	28	27
95% confidence limits (calculations made after Adams (1))	19–44	20–40

As with the sexually active adult males the difference between the numbers of females resident on the plot in the period prior to hatch in 1951 and 1952 is not statistically significant. Since it was impossible to mark all the females encountered on the plot, the figures obtained by actual count are low. The Lincoln index values are taken as best estimates and provide an average density of hens on the plot for 1951 and 1952 of 0.78 hens to the acre. Again, as in the sexually active adult males, the density is extremely high.

In comparing the average number of 17 adult males on Plot II in 1951 and 1952 with the average number of 28 adult and yearling females resident prior to hatch in the same time and area, it will be observed that the sex ratio is in the favor of females as 100:160. While this ratio is not statistically significant the disparity reflects the absence of yearling males from the breeding population and supports the conclusion reached by Bendell (5) that yearling males do not descend from the winter range in their first spring after hatch. Moreover, assuming the adult sex ratio 100:100, then approximately 30% of the hens are yearling birds. This figure for the age composition of the hen population is approached by another method below.

Fig. 1 (*a*, *b*, and *c*) represents the relative abundance of males, females, and females with brood over the years 1950 to 1953 as well as the seasonal trend of abundance of grouse on the summer range, i.e., the departure of the males from the breeding grounds and the hatch of the young. The differences observed among the curves from year to year are not considered indicative of a real change in numbers until week 15 or late July in 1950 as compared to 1951 and 1952, Fig. 1(*c*). The observed drop in these years reflects an early migration of hens and their broods in 1951 and 1952 or a delayed migration in 1950.

TABLE III

RELATIVE ABUNDANCE OF INCUBATING HENS AS INDICATED BY CLOCKER DROPPINGS

	1951	1952
Hours in field	311	222
Clockers found	104	62
Clockers per hour	0.33	0.28

The difference between the number of clockers found per hour in each year is not considered significant. The results of this census suggest that the relative abundance of incubating hens on the study area in the years 1951 and 1952 had not changed.

The results of all census methods are in accord and indicate that the number of adult males, females, and females with brood was virtually unchanged over the years 1950 to 1953. Thus in the period studied, these components of the blue grouse population at Quinsam Lake remained stable in numbers or their increase or decrease was not detected.

Each census method has its limitations. In counting territorial males, birds which abandon territory early in the year are not recorded unless censused appropriately. This situation is likely the cause of the variation in numbers of males on Plot II in 1953, Table I. Males hooting at the edges of the plot create a problem, for in this method, one observation might determine whether a male is in or out of a plot. In this study all territories on and touching the plot boundaries were counted. A count of males based on territorial activity ignores the male birds not holding territory. This error is corrected in part by the inclusion of all males observed per hour on the study area, as in the second census method. This method, as the count of clocker droppings, is limited mostly by the irregular activities of the observer, for any change in study technique from day to day influences the number and kind of observations made. The Lincoln index method of determining density of hens is biased by the movements of the females, which likely extended beyond the limits of the plot in which the census technique was used. If, however, movement of banded and unbanded hens into the census area equalled movement out, a not unlikely condition, then some of this error would cancel.

If the grouse population, as censused, is stable then several conditions would explain this stability or zero rate of population growth. The birth rate equals the death rate and emigration equals immigration. The birth rate is greater or less than the death rate and the difference between births and deaths is made up by emigration or immigration which results in population stability. Thus an explanation of the observed stability of population can be obtained from the consideration of death rates, birth rates, and dispersal in the study population.

Death Rate of the Adults

The death rate of adult males was calculated from time of banding in the spring and summer to time of observation the following spring. Since adult territorial males are easily observed and exhibit a strong homing tendency in years subsequent to banding (Bendell (5)), a percentage return can be

calculated. If males that do not return are assumed dead, the value represents a percentage survival. The number of males banded each year in the study area and the number returning in subsequent years is presented in Table IV.

TABLE IV

RETURN OF ADULT MALES EACH YEAR AFTER BANDING

No. banded each year	No. returned		
	1951	1952	1953
1950 : 19	12	9	6
1951 : 15		14	7
1952 : 8			5

The uniformity of the annual loss of males in the years subsequent to banding suggests a relatively uniform death rate, particularly in the case of the 1950 sample followed through three years. Despite the fact that birds banded in the three years were most likely to be of any one of several year classes, including birds two years old and older, analysis by Chi square indicates that the probability of a bird returning is not significantly different for the group or groups of birds banded or returned in any particular year. It would appear then that death occurred independently of age. Farner (11) has shown a tendency in some birds towards uniform mortality rates which do not vary extensively with age after a period of higher mortality in the juveniles is passed. This seems true of the adult blue grouse. Mortality in the young will be discussed below.

As a best estimate of return of the adult males each year the total number of males returned is expressed as a percentage of the total number of males banded or returned prior to 1953. This calculation gives a 69% return each year. Assuming that males that do not return are dead, the value represents a 69% survival each year or a 31% yearly death rate in the territorial adult male. This is a low death rate for a gallinaceous bird.

In the case of females, failure to observe a hen in years subsequent to banding cannot be taken as indication of the bird's death. There is evidence to suggest that like the adult males, some females return year after year to the same locality on the summer range; however, unlike the males they do not become localized on a territory. Further, most of the banded females were captured when with their young and thus probably were far from the relatively small range they occupied prior to and during incubation. The chances of observing such hens in years subsequent to banding are even less

than of observing the few hens captured and banded before or during the incubation period. In the absence of other data, the yearly death rate in females is assumed to be that found in adult males, 31%.

Mortality Factors in the Adults

The factors that operate to remove the females and adult males from the population are largely unknown. In the case of marked adult males, none was found dead on its territory; rather their numbers remained unchanged throughout the spring and summer except as affected by what is taken as the abandonment of territory at the cessation of sexual activity. However, some mortality of the adults does occur on the summer range. Over the years 1950 to 1953 the remains of seven adult birds and one yearling have been found in the study area. From faeces, hair, feathers, and odor found near the remains it would seem that fox (*Vulpes fulva* Desmarest) and an avian predator could be involved. In the spring of 1950 a fox and two pups were discovered beside a den in the edge of an old railway embankment. The ground in and about the den was littered with the remains of grouse. These remains were classified on the basis of feather color and shape as the parts of 12 adult males and three adult females. This would suggest, if the sample is valid, that predation by fox is heavier on males than females, an observation in accord with the relative ease of locating and capturing hooting males in spring.

The Quinsam area is hunted for grouse and black-tailed deer (*Odocoileus hemionus columbianus* Richardson). Accordingly, human predation might be a factor contributing to the mortality of adults and chicks. However, hunting has little or no effect on the adult male component of the population because of the early upward migration of the adult males which occurs in August and the weeks before the opening of the grouse season in September. Thus of 204 adult birds sampled at random from hunters' bags in 1950, but four were males.

Human predation has more effect on the breeding females and their chicks, which bear the brunt of the shoot. There is no clear indication, however, that the entire population of females and their broods suffer a uniform mortality from hunting. There is the possibility that like the males, some hens and young escape hunter predation by an early upward migration in August. For this analysis, however, let us assume that all banded females are subjected to uniform hunting pressure and that all banded hens killed are reported. The second condition was probably fulfilled since the take of most hunters of the Quinsam area was checked during the periods of greatest harvest. The percentage of banded hens shot each year during a three year study period is presented in Table V.

TABLE V

NUMBER OF BREEDING HENS BANDED AND SHOT IN EACH STUDY YEAR

Year	No. banded	No. shot	% shot
1950	61	2	3
1951	27	0	0
1952	20	0	0

From this it would appear that the loss to hunting was negligible and was a minor factor contributing to the 31% yearly turnover assumed for the adult and yearling hens. This conclusion is supported by a consideration of the sex ratio on the range in spring. If the shoot were having an effect on the adult and yearling female component of the population, one would expect a disproportionate sex ratio in the breeding range in favor of adult males which escape the harvest by their earlier altitudinal migration. As mentioned above, the ratio of males to females on one plot in 1951 and 1952 was 100 : 160.

Disease does not appear to be a major mortality factor in the adults and yearlings, at least on the summer range. This statement is based upon the examination of 174 blood smears taken from shot or captured birds and upon 103 autopsies. In the birds sampled, behavior, weight, and conditions of the organs and body were checked for disease symptoms. Although ecto- and endo- parasites were commonly found, symptoms of disease were not observed. The parasites found in the adults and yearlings are listed in Table VI.

It is noteworthy that despite the high percentage and degree of infections recorded for blood parasites no apparent effect on the host was observed. *Dispharynx nasuta*, *Plagiorhynchus formosus* (occurring in chicks), *Yseria*, sp., *Cheilospirura spinosa*, *Ascaridia bonasae*, and *Ceratophyllus diffinis* are new host records for the genus *Dendragapus*. The percentage of birds infected and degree of infection with *Dispharynx* and *Plagiorhynchus* in the adults and yearlings is in extreme contrast with the severe infestations of these worms recorded in the chicks and will be mentioned again below.

What effect parasitism might have on the adults once they are in the highlands and under the greater climatic stress of winter is an interesting question. With the lack of other evidence from the summer range it seems likely that the greater part of the 31% yearly mortality recorded in the adult males and assumed for adult females occurs on the winter range. Here predation or some combination of predation, weather, and debilitation through disease might act to produce a major portion of the observed yearly loss or turnover.

TABLE VI

PARASITES OF ADULT AND YEARLING GROUSE EXAMINED DURING SPRING AND SUMMER OF 1950, 1951, AND 1952

Parasite*		No. examined	No. infected	% infected	Degree of infection
Haemoproteus sp.	Sporozoa	174	169	97	1–500 per 1000 r.b.c.
Leucocytozoon sp.	Sporozoa		148	85	1–2 per 1000 r.b.c.
Trypanosoma sp.	Mastigophora		134	77	1–20 per smear
Microfilaria	Nematoda		139	80	1–25 per smear
Quadruple infections			99	57	
Dispharynx nasuta Rud.	Nematoda	103	4	4	1–6
Cheilospirura spinosa Cram, *Yseria* sp. †	Nematoda		23	22	1–5
Rhabdometra nullicollis Ransom	Cestoda		40	39	1–20
Ascaridia bonasae Wehr	Nematoda		14	14	1
Plagiorhynchus formosus Van Cleave	Acanthocephala		0	0	
Ceratophyllus diffinis Jordan	Siphonaptera		11	11	1–4
Lagopoecus obscurus Emerson(?)	Mallophaga		39	38	1–300
Ornithomyia fringillina Curtis	Diptera		2	2	1–2

* *For site found see Table XI.*

† *These nematodes, macroscopically alike, were not differentiated in autopsies. C. spinosa is the more commonly occurring form. A new species of Yseria is yet to be described and named.*

‡ *Occurs in chicks.*

Death Rate of the Young

The death rate of the chicks or young of the year was studied in terms of decrease in brood size from the time of hatching until the middle of August in each study year. Time of peak hatch was taken as June 15 to June 21 (Bendell (5)). The number of chicks observed in each brood was tallied and an average size of brood calculated for each week. The results are presented in Table VII.

TABLE VII

AVERAGE SIZE OF BROOD CALCULATED FOR EACH WEEK OF 1950, 1951, AND 1952

Week	1950		1951		1952	
	No. broods	Av. size	No. broods	Av. size	No. broods	Av. size
June 15–21	3	1.7	14	2.5	9	3.3
22–28	6	4.0	19	3.3	5	3.2
29–5	7	2.7	12	4.3	11	3.3
July 6–12	21	2.9	21	3.6	14	2.6
13–19	25	2.4	25	2.6	28	1.9
20–26	19	2.4			6	2.5
27–2	55	2.7	4	2.7	18	2.1
August 3–9	28	3.2	11	1.8	9	2.0
10–16	44	3.2			13	1.5
17–23	9	3.8			7	1.7

The differences between the weekly averages of each year from June 15 to Aug. 2 are not statistically significant. By the week of Aug. 3-9, however, the averages of 1950 are at variance with the averages of 1951 and 1952. The best explanation for this is that in August of 1950, unlike 1951 and 1952, a tendency towards disorganization of the broods occurred in the hens and young. Under these conditions it became impossible to count accurately the progeny of any one female. Brood size per hen for that year is taken as 2.7, the average size of 55 broods observed in the week of July 27 to Aug. 2.

In each year the average size of brood increased from the week of hatch to a high between weeks June 22 to July 5. In the first week after hatch, when a brood is observed, some chicks escape detection through the violent diverting action of the female and by remaining motionless or darting under logs and debris. By the third week after hatch, the chicks tend to run and flush readily when a brood is discovered. Thus relatively accurate counts are possible. From this and the above consideration of 1950 data it is evident that there is a pronounced drop in brood size from the average clutch of six eggs per hen (Bendell (5)) to approximately two chicks per hen by August—a 67% decrease in size of brood. This death rate in chicks or reduction of productivity per hen is actually greater than 67% for in counting the chicks of hens with broods, females that are seen without broods are not tallied. Some of these females have lost all or did not have any young. It is

not possible to consider the number of hens seen alone as the number having no brood for females with chicks are more readily heard and observed because of their behavior and their reaction to an artificial call of a chick in distress as produced by the observer.

As an estimate of the number of unproductive females and females which lose all young on the study area the census data of Fig. 1(*b*) were used in the following manner: Assuming that all females observed alone per hour in the weeks Apr. 13 to July 19 (weeks 1 to 14) are resident females and that such females are as readily observed in the spring weeks as in the summer, then the average number of females observed alone per hour in weeks Apr. 13 to May 24 (weeks 1 to 6) to the average number of females observed alone per hour in weeks June 15 to July 19 (weeks 10 to 14) is a ratio of females on the range in spring to unproductive females and females which have lost by death all young on the range in summer. The periods Apr. 13 to July 19 and June 15 to July 19 were selected for several reasons. One reason was to remove any bias created by nesting hens in the approximately three weeks of incubation. This activity would remove them from the observed population of hens and bias the ratio in favor of productive hens. This bias would again occur after July 19 for there is indication from the figure and the behavior of the adult males, that after this time, unproductive hens and hens that have lost all their chicks leave the summer range.

From the data of 1950 to 1952 the average number of females observed alone per hour in weeks Apr. 13 to May 24 is 0.55. The average number of females observed alone per hour in weeks June 15 to July 19 is 0.22, a figure representing the number of unproductive hens and the hens that have lost all their young in the study area between time of hatch and July 19. Thus 0.22/0.55 or 40% of the females are without young in the weeks of the summer up to July 19. The brood size of the remaining hens is reduced by 67% by August. Assuming that there is no further mortality and that each hen has produced six chicks then 80% of the chicks die in the first three months after hatch.

It is now possible to calculate the reproductive success of the hens on the study area in terms of the number of chicks per hen by August. The number of chicks per hen by August can be integrated with the data on the stability of the population, the death rate of the adults, and the survival and dispersal of the chicks to explain the stable population of blue grouse as observed at Quinsam Lake.

In a hypothetical 100 hens on the study area in spring, 40% are without broods by July 19. By August the remaining 60% of the hens have broods of two chicks. Thus by August 100 hens have 120 chicks. If now 31% is taken as the winter turnover in the 100 hens and assuming no further change in the numbers of chicks and a 100 : 100 sex ratio as observed in the young (Bendell (6)), by the following spring the hen population should consist of 129 birds (60 yearlings and 69 adult hens), a condition in which the yearlings make up 47% of an increasing population of hens. The situation would be

similar in the males. This conclusion is rejected for as noted above the population of females and adult males in the study area has remained stable over the four year study period. Moreover, yearlings do not make up nearly 50% of the population of hens.

To determine the percentage of yearlings in the population of hens, 66 hens were shot or captured at random before incubation had begun in the years 1951 and 1952. The results of the sampling are summarized in Table VIII.

TABLE VIII

PERCENTAGE OF YEARLING HENS IN THE POPULATION OF HENS ON THE BREEDING RANGE IN SPRING

Year	Sample size	No. yearlings	% yearlings
1951	25	6	24
1952	41	11	27
Total	66	17	26

From this, it may be seen that the percentage of yearlings occurring in the population of hens is not, at 26%, the 47% predicted above for an increasing population but is closer to the 31% which would replace the yearly loss assumed to occur in hens a year or more old. Thus to maintain the observed stable population and produce an expected 31% yearling hen class in this population another 57, or 47%, of the 120 chicks surviving to August must die between August and the following spring, migrate to regions remote, or do both. Indirect studies on dispersal (to be discussed below) suggests that dispersal is relatively unimportant as a control of population. A consideration of the 31%, presumably winter turnover in the adults, and the causes of mortality in the chicks (to be discussed below) supports the view that a further 47% mortality of the young occurs between August and the following spring.

Dispersal

Observations on banded breeding adults showed that this portion of the population returns each year to the same locality of the summer range until presumed dead (Bendell (5)). There is no direct evidence to show that the young of this localized breeding population return to the locality of birth. A total of 37 chicks was banded in the study area in 1950 and 1951. None was recorded on the summer range in subsequent years. One explanation for this, other than emigration, would be the large mortality occurring in early life before and after hunter predation. Another explanation could be the distance (up to one-half mile (5)) of the chicks from their nests at the time of banding. If the banded chicks did return to the region of their nests in subsequent years this region might be outside of the study area. Thus discovery of the birds would be unlikely.

Nice (16) has shown that yearling song sparrows (*Melospiza melodia* (Wilson)) tend to return to the locality of birth. Such a return has been demonstrated in other, but not all, studies of banded birds. Nice suggests however that if, on the return of the young song sparrows, some factor such as space is limiting, the birds move on to new locations.

Assuming that young blue grouse do return to the region of their birth there is no apparent reason why they should leave it or why immigration into the study area from other places should not occur. This seems most obvious in the case of breeding hens for which food, protective cover, and nesting sites appear in abundance at Quinsam lake. Moreover, no behavior mechanism has been observed in the hens which might limit their density in a given area. Since the cocks are polygamous (Bendell (5)) the limitations imposed by monogamy can be dismissed as a factor contributing to the control of population.

Many authors have stressed the importance of territorial behavior in male birds as a mechanism capable of limiting population. Stewart and Aldrich (20) attempted to eliminate the population of breeding birds from a sample area in a spruce–fir forest. As one male was shot, however, another took its place. They concluded from this that most of the space suitable for territories was occupied before shooting began and the rapid replacement of new males came from a "floating" population of birds which had lost in the competition for space to other members of their species. They agree with Nice (16) who states, "It (territory) ensures that there will be no crowding and no overpopulation since surplus birds must go elsewhere."

To test this condition, in May of 1952, 16 hooting males were removed from an area of approximately 60 acres. Two banded males were left in the area as "inducers" with the belief that their hooting would influence members of a "floating" population to settle. In no case was an emptied territory reoccupied in that year. The two banded birds remained throughout the summer as the only resident males. In June of 1953 the area was recensused. One banded male was replaced and three new arrivals occurred on the area in regions where territories had not been recorded in the years 1950 to 1952. On the basis of 18 males on the area in 1952, a 31% turnover, and a stable population, the number of new arrivals was predicted at six. As noted above, four occurred and approximately equalled the 31% loss of adult males. This left vacant 13 areas suitable for territories. If then young blue grouse return to the region of their birth there is no apparent reason why they should not remain as breeding birds.

Alternatively there is no apparent reason why young grouse from other regions than Quinsam Lake should not become located as breeding birds in the study area. The simplest explanation for the number of new birds in the study population each year is that the new birds represent the surviving young and dispersal is zero. With the lack of other evidence on the movements of young prior to their localization as breeding birds and in view of the causes of mortality in the young (to be discussed below) it would appear,

as concluded above, that a further 47% mortality occurs in the chicks that survive the period from hatch to August, and that this occurs before the following spring.

A Life Table for the Study Population

From the conclusions reached above, the stable population observed on the study area can be explained as a condition wherein (1) 40% of the females are unproductive or lose all young, (2) 60% of the females lose four out of six or 67% of their young in the summer months, (3) the surviving young have a 47% fall and winter mortality which reduces their numbers to a level that equals the 31% yearly loss observed in the older age classes and results in the observed stable population.

With these data the population dynamics of the blue grouse at Quinsam Lake can be summarized in a life table and a survivorship curve, Table IX, Fig. 2. The life table begins with a theoretical 1000 eggs in the nest. The first loss is from broodless females which may have been unproductive or have lost all their young. Strictly speaking the loss of eggs through non-

TABLE IX

LIFE TABLE FOR THE BLUE GROUSE AT QUINSAM LAKE

Primary data	Survivors	*x* (age in years)	*lx* (cohort of 1000)	*dx*	*qx* (%)
Eggs of 100 females	600	0	1000		
Loss of complete brood	360		600	400	40
Loss of chicks over the summer	120		198	402	67
Loss of chicks from fall to spring	63	1	105	93	47
31% loss of adults each year	43	1–2	72	33	31
		2–3	50	22	
		3–4	34	16	
		4–5	23	11	
		5–6	16	7	
		6–7	11	5	
		7–8	8	3	
		8–9	6	2	
		9–10	4	2	
		10–11	3	1	
		11–12	2	1	
		12–13	1	1	
		13–14	0	0	

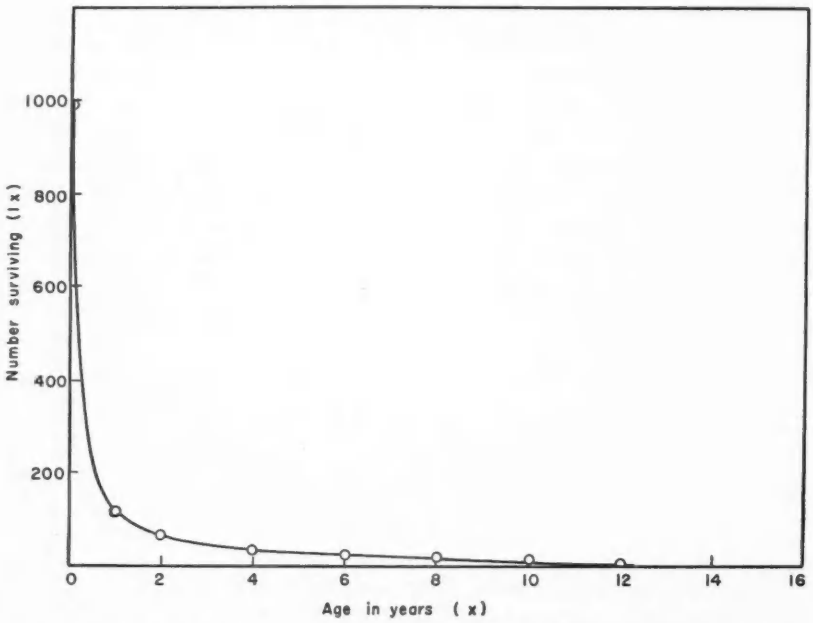

FIG. 2. A survivorship curve for the blue grouse at Quinsam Lake, 1950 to 1953.

productivity of hens occurs before or without nesting and should not be considered in a table which begins with a theoretical 1000 eggs in the nest.

Fig. 2 drawn from the data in Table IX can be called a survivorship line. It is a negatively skewed rectangular curve or a concave "J" in shape. This reflects the production of a large number of eggs by a single female, extremely heavy mortality in the early stages of life, and a relatively uniform death rate thereafter. It seems likely that these conditions are true of most birds although few other data are available on the mortality of birds from nest to first year of life—the critical period. According to Hickey (13) the only approach to this negatively skewed curve thus far reported for birds is found in Deevey's (9) reanalysis of Nice's (16) work on the song sparrow.

Mortality Factors in the Chicks

The life table calculations begin with the supposition that each female on the summer range lays six viable eggs. There exists the possibility that some females do not lay or in so doing produce non-viable eggs. Either condition might account for the 40% broodless females observed on the study area. As an analysis of this situation in the spring of 1951 and 1952, 61 hens were shot or captured at random, their age was determined, and they were examined for breeding condition. The results are listed in Table X.

TABLE X

PERCENTAGE OF BREEDING HENS IN EACH AGE CLASS

Age class	Number in sample of 61 hens	Breeding criterion and number of hens classed by it	Number breeding	% breeding
Yearling	13	Brood patch 2 Ripe ova 2 Shed follicles 5	9	70
Adult	48	Brood patch 7 Ripe ova 5 Shed follicles 34	46	96

There is a statistically significant difference between the number of yearling and adult hens engaged in breeding activity. On the basis of this sample, 70% of the yearling hens and 96% of the adult hens are productive. If then, yearlings make up approximately 26% of the hen population (Table VIII) then in 100 hens on the spring range 18 are breeding yearlings and 71 are breeding adults, that is, 89% of the females in the study are are breeding or productive birds.

This situation is reflected in the relative number of each age class found with broods. In sampling hens with young it was assumed that each age class was as likely as any other to lose nests and young and each was sampled without bias or with the same bias. From the above calculations the ratio of yearlings with chicks to adults with chicks, after the hatch, should be 18 to 71 or 0.25. In 1951 and 1952, 48 females were shot or captured when with broods. Of these, nine were yearlings and 39 were adult hens, a ratio of 9 to 39 or 0.23. The deviation from the expected ratio is not statistically significant.

If 89% of the hens in the summer range are productive then non-productivity alone does not explain the 40% observed without broods and suggests that most loss of young occurs after the eggs are laid.

Data on the number of addled or infertile eggs laid by nesting hens are meager. Of 36 nests found on the study area but three contained addled eggs—one egg in a clutch of six, two in a clutch of seven, and two in a clutch of four. While addled eggs may have been left in the other 33 nests they could have been destroyed or carried away by predators before the nests were discovered. From other studies on gallinaceous birds infertility of eggs has not been a major factor in the loss of chicks. While this unexplained phenomenon may help decrease brood size by a chick or two, it is not considered as a sole factor creating loss of broods from the study population.

Nest desertion and/or predation appears to be a relatively important factor in the mortality of young grouse before they hatch. This conclusion is based upon the fate of the 36 nests discovered over a three year study period.

Of the 36 nests only six were found prior to successful hatch or destruction. The remaining nests were classified as to a successful or unsuccessful hatch on the basis of shell fragments in and around the nest. All the nests classified as unsuccessful showed evidence of predation but in such nests desertion might have occurred before depredation. In the six nests mentioned above, two were lost through predation rather than nest desertion. In the absence of data to the contrary, it thus seems likely that the failure of most nests is a direct result of predation rather than desertion.

In the sample of 36 nests, nine or 25% were lost apparently through depredation. This figure, while not high in comparison with other studies, is probably greater than the number of nests actually destroyed. When a nest has been destroyed the eggs are broken and scattered about in a manner that aids in the identification of the predator and the discovery of the nest. After a successful hatch the shells are relatively undamaged and remain hidden by logs and vegetation within the nest. Doubtless these 'successful' nests are less often found than the 'unsuccessful', a condition that introduces an unknown bias into the calculation in favor of destroyed nests.

Identification of nest predators on the study area is based on circumstantial evidence. Bump *et al.* (7) describe and illustrate nests of ruffed grouse (*Bonasa umbellus* L.) destroyed by various animals. From the descriptions of Bump *et al.* and from faeces, hair, feathers, and odor at the nine destroyed nests an attempt was made to identify the predator, which seems to have been: for one nest, fox; four, fox or raccoon (*Procyon lotor* L.); one, raven (*Corvus corax* Ridgway); and three, unknown.

From the above considerations it is evident that non-productivity and nest depredation are not the sole causes of the 40% broodless females observed on the study area. Moveover, these factors do not explain the 67% drop in size of broods over the summer months. Clearly, both conditions are a result of mortality in the young after hatch.

The pattern of mortality in the chicks, as recorded in Table VI, has been similar over the years 1951, 1952, and early 1950, with a downward trend in the average size of broods from the last week in June to the end of field observation. The gap in reliable data on size of broods between time of hatch and the end of June leaves much to be desired. It might be assumed that the trend begins at six eggs in the nest and follows the same "slope" of mortality as in the older age classes. On the other hand, conditions peculiar to survival in early life might be acting to remove young birds from the population and cause a sudden drop to what is observed as maximum size of brood by the first of July. Addled eggs or sickly chicks which perish shortly after the hatch might be considered as causes of loss of young in early life.

Beer (2), Fowle (12), and others report blue grouse chicks to be insectivorous in diet until about 10 days of age when they begin to take vegetable food. While plant material is obviously plentiful at Quinsam Lake, a shortage of acceptable invertebrates might exist and this, caused by or associated with inclement weather, might remove week-old chicks from the broods. It is noteworthy, however, that the decrease in average size of brood continues beyond late June and early July despite the fact that the chicks by this time are on a vegetable diet.

Inclement weather per se, or in association with a shortage of food, might result in the death of week-old grouse, particularly if a chick became separated from the brood. Thus the first three weeks of life can be considered critical with respect to the effects of weather on the survival of chicks. Weather records were obtained in each day of the critical three week period in 1951 and 1952 by thermograph and rain gauge and by recording the duration of rainfall in days. Minimum temperatures and rainfall were averaged for the week. Duration of rainfall is expressed as total days of rain in the week. The average weekly minimums for 1952 when totalled were 8° F. less than the total for 1951. Rainfall in 1952 was greater by 0.2 cc., and occurred over six more days than in 1951. However, assuming other mortality factors to be the same in each year, the relatively wet weeks of 1952 did not have a deleterious effect on brood size as compared to 1951, Table VI.

The role of predation in reducing the size of broods is largely unknown. Avian and mammalian predators occur and doubtless remove chicks from the broods, but direct and indirect evidence of loss of chicks to predators is almost completely lacking. There is no reason to believe that predation by birds and mammals is an important mortality factor in early life. On the other hand the fall harvest by hunters is an apparent cause of mortality to the chicks. From road check data (Taylor, E., unpublished B.C. Game Report, 1950) chicks formed a minimum of 80% of the total bag checked in 1950. Thus four chicks are shot for every hen. If the hunter success in taking females in 1950 to 1952 is averaged as 1% (Table V) then this would suggest that 4% of the chicks are shot.

In 1950 and 1951, 37 chicks were banded and released. Assuming the sample present on the summer range prior to harvest to be intact, an unlikely assumption, the number shot as related to the number banded gives some indication of hunter success. Of the 37, three or 8% were shot and reported by hunters. This would be a minimal figure as some of the original 37 probably died before the shoot. However, from the above and the apparently negligible loss of breeding hens, which would be more sensitive to hunting pressure than the chicks, it is concluded that predation is not an important mortality factor in the young on the summer range.

Within this gamut of apparently minor causes of chick destruction, disease is clearly evident as an environmental factor capable of crippling and killing chicks. Table XI summarizes the parasites found in chicks collected from time of hatch to the end of August in the years 1950 to 1952 at Quinsam Lake. The data in Table XI are from 89 chicks from which blood smears were taken for examination of the blood and 107 chicks autopsied for visceral parasites. Not included in the table is the record of one tick (*Ixodes auritulus* Neumann) removed from the head of a chick examined at the 1950 road check at Campbell River. In the summer of 1950, bacterial infections occurred in 10 out of a sample of 60 chicks examined in the field. The infections were apparently caused by mechanical injury to the feet and other body parts with subsequent bacterial invasion. Similar cases were not recorded in 1951 and 1952.

TABLE XI

PARASITES OF CHICKS COLLECTED AT QUINSAM LAKE FROM TIME OF HATCH TO THE END OF AUGUST. POOLED DATA OF 1950, 1951, AND 1952

Parasite	Site found	No. examined	No. infected	% infected	Degree of infection
Haemoproteus sp.	Blood	89	59	66	1–50 per 1000 r.b.c.
Leucocytozoon sp.	Blood		34	38	1 per 1000 r.b.c.
Trypanosoma sp.	Blood		18	20	1–10 per smear
Microfilaria	Blood		0	0	0
Triple infections			5	6	
Dispharynx nasuta	Stomach	107	68	64	1–430
Cheilospirura spinosa *	Gizzard		11	10	1–2
Yseria sp. *					
Rhabdometra nullicollis	Gut		22	21	1–20
Ascaridia bonasae	Gut		4	4	1
Plagiorhynchus formosus	Gut		53	50	1–33
Ceratophyllus diffinis	External		0	0	0
Lagopoecus obscurus (?)	External		21	20	1–50
Ornithomyia fringillina	External		7	7	1–2

* *These nematodes, macroscopically alike, were not differentiated in autopsies. C. spinosa is the more commonly occurring form.*

Note in comparing Table XI with Table VI, the parasites recorded in the adults and yearlings, that several differences occur. Generally, the incidence and degree of infection are lower in the chicks. This is probably more apparent than real since the sample of chicks would include young birds which might be in a prepatent period of a particular parasite attack or carry a low grade infection. Microfilaria were absent from the blood of chicks over the period studied.

TABLE XII

OCCURRENCE AND DEGREE OF *Dispharynx* AND *Plagiorhynchus* INFECTIONS IN CHICKS SAMPLED BY WEEKS. POOLED DATA 1951 AND 1952

	Weeks from week of peak hatch (June 15–21)							
	1	2	3	4	5	6	7	8
Sample size	14	10	13	15	15	10	21	9
No. infected with *Dispharynx*	2	4	6	13	14	7	17	5
% Infected	14	40	46	87	94	70	81	56
Average No. worms per infection and Range	2 (1–2)	6 (2–14)	42 (12–100)	60 (13–200)	44 (2–136)	27 (2–50)	86 (1–430)	69 (2–175)
No. infected with *Plagiorhynchus*	2	3	6	10	11	6	11	4
% Infected	14	30	46	67	73	60	50	45
Average No. worms per infection and Range	1 (1–2)	1 (1)	11 (3–33)	8 (3–20)	5 (1–13)	4 (1–9)	12 (1–47)	10 (7–15)
No. chicks infected with both parasites	1	1	6	8	11	4	10	4
% Infected	1	1	46	53	73	40	48	44

A striking and important difference between parasitosis in the chicks and adults is observed in the occurrence of *Dispharynx* and *Plagiorhynchus* as common parasites of the young. The four *Dispharynx* infections recorded in Table VI occurred in three yearlings and one adult bird with the degree of infection from one to six worms. *Plagiorhynchus* was not found in adult or yearling grouse. Note in Table XII, in the chicks collected four to five weeks after time of hatch, that 87–94% were infected with *Dispharynx* and 67–73% were infected with *Plagiorhynchus*. Moreover, in this time, 53–73% of the chicks examined carried both worms.

Dispharynx and *Plagiorhynchus* were the only parasites encountered which created obvious damage in the grouse. The fact that both worms have Isopoda as their Intermediate host (Sinitsin (19), Cram (8)) may explain the high frequency of occurrence and association of the two parasites since isopods are a common item in the diet of chicks.

Dispharynx occurs in the proventriculus of grouse and causes extreme damage. In severe infestations of 100–300 worms, the proventriculus is diseased and proliferated into long fibrous shreds. These and profuse quantities of mucus occur in the lumen of the stomach creating a barrier to the passage of food. The worms are found in this tissue or embedded in the glands of the stomach which are, in most cases, devoid of secretion. The stomach often enlarges to four times its healthy size and is streaked and blotched with red inflammation as compared to its normal light gray or beige color.

The acanthocephalan *Plagiorhynchus* has its habitat in the lower small intestine of chicks and while not associated with as great a host reaction as recorded for *Dispharynx* still creates obvious damage to the tissues of the gut. The worm generally occurs with its head of spines embedded in the intestinal wall. Twelve cases have been observed where the gut was perforated and the worms free in the coelome or under the intestinal mesentery. Usually the gut is constricted and thrown into a tight coil at the site of infection and apparently blocks the lumen.

Chicks with severe infections of *Dispharynx* and *Plagiorhynchus* or *Dispharynx* alone are emaciated, weak, and easily caught in the field by hand. Their body organs, especially the kidneys, appear blanched and pale, while the intestine is filled with a slimy liquid and gas. Five young grouse, apparently near death from the ravages of these worms, were collected in the study area.

What converts an infection with *Dispharynx* or *Dispharynx* and *Plagiorhynchus* into a lethal condition is unknown. Edminster (10) considers 20 to 30 *Dispharynx* capable of affecting the health of ruffed grouse while more may prove fatal. He designates this parasite a major pathogen when it

occurs. As illustrated in Fig. 3, infections with 20 and more *Dispharynx*, not considering *Plagiorhynchus*, are commonly encountered. Host–parasite relationship is made more complex by introducing the effects of age, host resistance, other parasites, weather, predators, and food supply as additional variables. One or a combination of these factors might tip the balance of an infection with *Dispharynx* from recovery to death.

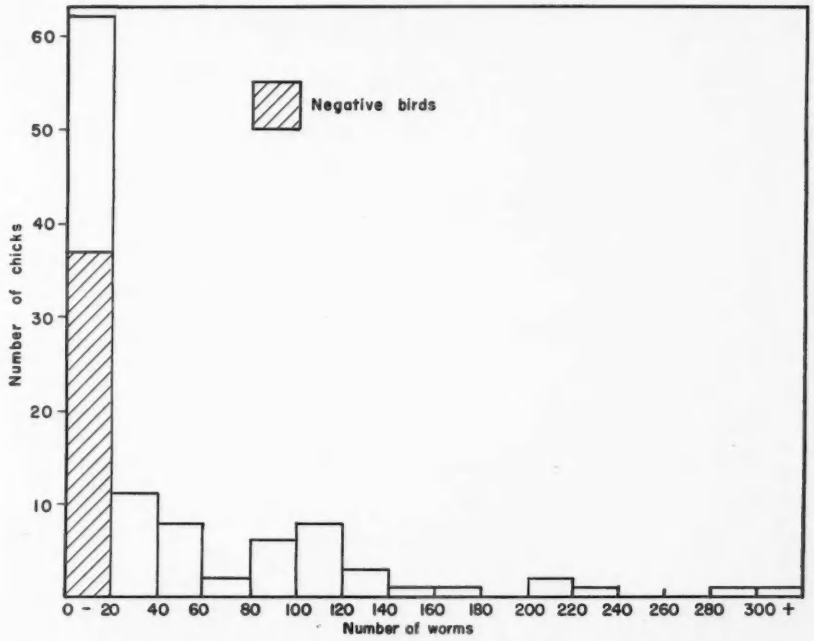

FIG. 3. Distribution of infections with *Dispharynx* in a sample of 108 chicks autopsied at Quinsam Lake. Data of 1950, 1951, 1952, and 1953.

The pathogenicity of *Dispharynx* and *Plagiorhynchus* infections cannot be doubted. There remains to be shown a correlation between mortality of the chicks and parasite attack. The downward trend in average size of broods from the end of June of each year has been noted above. It is worthwhile to consider the variates of each week's average as an explanation of the observed drop. Fig. 4 illustrates the frequency of occurrence of size of brood in each week from June 29–July 5 (week 12) to Aug. 17–23 (week 19) in 1950 and 1952. The 1950 data, hatched in the diagrams, are unreliable. Note that with week 14 the figures become skewed to the left so that a brood size of one is the modal class or becomes a relatively frequent size of brood thereafter. The occurrence of one chick per brood would indicate the previous loss of young. It would also suggest that total loss of young occurs and results in hens without broods.

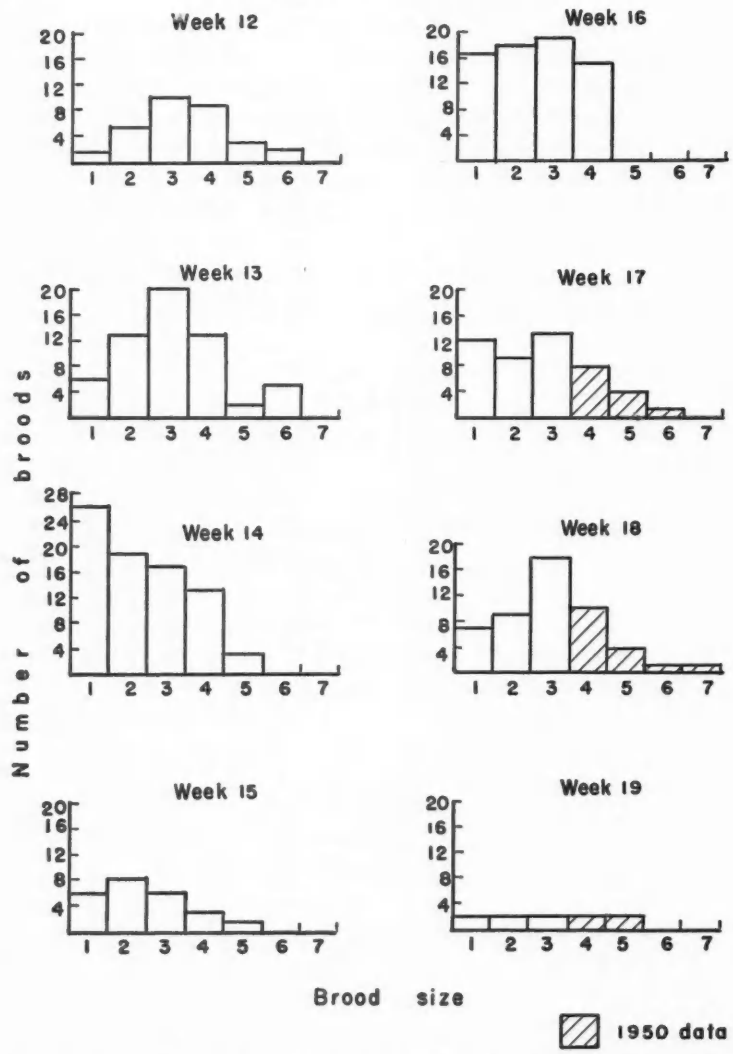

FIG. 4. Histograms comparing distribution of brood sizes for weeks June 29–July 5 (12) to Aug. 17–23 (19). Data of 1950, 1951, and 1952.

The increasing frequency of occurrence of small broods on the study area correlates well with the build-up of *Dispharynx* and *Plagiorhynchus* infections in terms of percentage of young infected and average number of worms per infection with each week of study, Fig. 5 from Table XII. The correlation coefficient r is .811, $P < 10\%$ (calculated between the average weekly size of broods from June 29 to Aug. 2 (week 12–16) in 1950 to 1953, and percentage

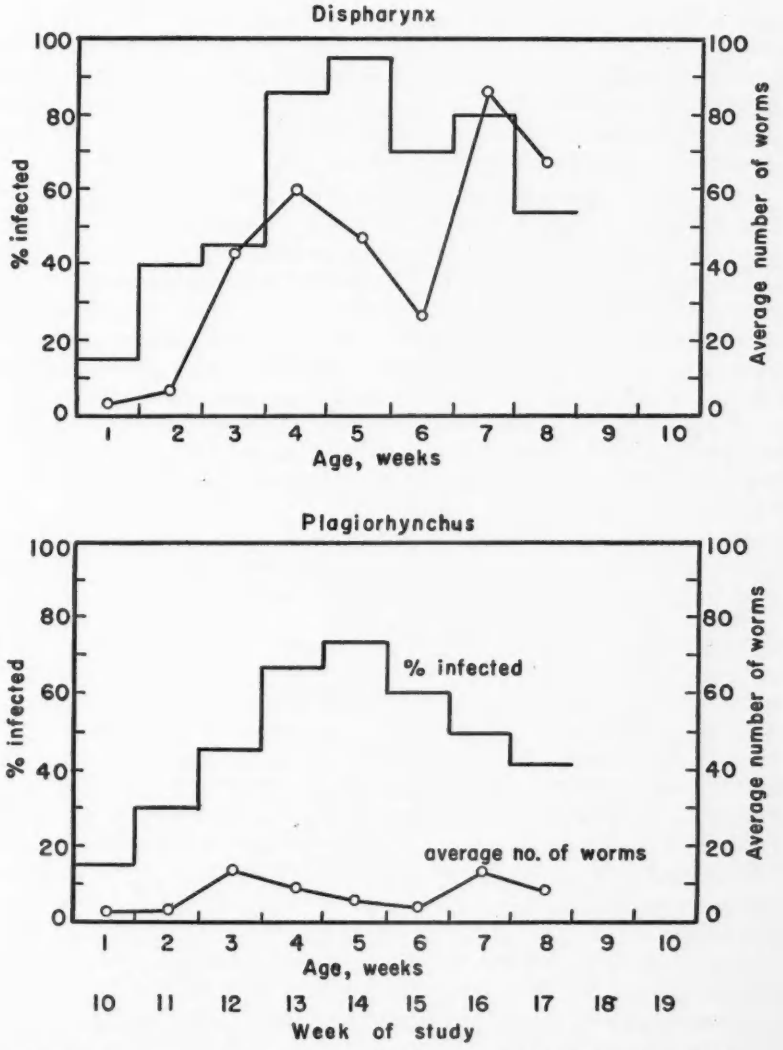

FIG. 5. Percentage of chicks infected with *Dispharynx* and *Plagiorhynchus* and degree of infection with age and week of study. Data of 1950, 1951, and 1952.

chicks infected with *Dispharynx* in each week of this period over the three years). Peak infection with both parasites occurs in the week July 13–19 (week 14) or when the chicks are five weeks of age. By week 14, as noted above, a brood size of one is the modal class and many hens are probably broodless. After the middle of July (week 15) there is a downward trend in the number of chicks infected with the two helminths, a condition which

might reflect the removal of heavily infected birds from the population, a developing immunity in the young as they grow older, or both. Nevertheless, in a sample of 16 chicks obtained at Quinsam Lake in September of 1950 and 1951, 12 were infected with from one to 300 *Dispharynx*, while six were infected with from five to nine acanthocephalans, an indication that these parasites are carried onto the winter range.

There is then a correlation between parasitic infestation and death of chicks. In view of the 89% productivity of the hens and of the non-discovery of any other factors seriously affecting the young, it seems logical to conclude that the parasites *Dispharynx* and *Plagiorhynchus* are causal agents of the extreme mortality recorded in the chicks and in turn, major factors affecting the density and stability of the population in the study area. Death from disease would explain in most part the occurrence of the 40% broodless hens and the 67% loss of chicks per hen recorded on the summer range. Moreover, it would seem likely that chicks carrying these parasites would suffer greater mortality under conditions of winter stress than would the older age classes. This mortality was calculated at 47% between fall and spring as compared to a 31% yearly mortality in the older birds.

Discussion

The conclusions reached above are subject to criticism on two points at least. The sampling methods used and the small samples obtained make interpretation of the results hazardous. However, there is some reassurance in the fact that many of the arguments are supported by independent data which lead to similar conclusions. As a second point, while disease in the chicks appears to be a major cause of mortality, this cannot be considered the only environmental factor important in control of the blue grouse population. With the lack of other evidence it is stated that disease in the chicks is the most important cause of death and as such is the limiting factor to the present density and growth rate of the population.

Food conditions are generally accepted as the prime factor regulating animal populations. While food supply is obviously involved, it cannot be considered a factor of major importance in control of the blue grouse population at Quinsam Lake. Similarly, space, predation, and weather factors have relatively minor effects on the present form of growth of the population.

The present density of blue grouse at Quinsam Lake deserves further comment. Unfortunately densities of blue grouse in undisturbed coast forest are not known with any accuracy. The author spent two weeks at Cowichan Lake, an area more advanced in burn succession than Quinsam Lake, with some original forest still present. Here densities of grouse were low as compared to those in the study area. In looking for an underlying cause of the relatively high density of population at Quinsam Lake it would appear that the early stages of burn succession found there were more favorable environment for blue grouse. From a consideration of the various

types of habitat utilized by the adult birds it is evident that they have a relatively wide environmental tolerance. They are apparently free of disease and exist in an abundance of food at all seasons. Predation is probably the greatest cause of mortality in the adults. The chicks then are the vulnerable "link" in the "population chain". Thus the relatively high density of grouse at Quinsam Lake can be explained as the result of a change in the original forest which now provides more suitable conditions for the chicks. These changes would be primarily in food supply and in the structure of the vegetation.

The chicks, however, bear the brunt of mortality factors and in this case extreme mortality from disease is a major factor in present population stability. On the basis of this observation, the growth and control of population depends mainly on the conditions affecting the welfare of the young.

Leopold (14) has suggested that blue grouse populations are cyclic in numbers with a 10 year period between successive peaks. Wing (22) has remarked on the fluctuations which occur in populations of blue grouse. Fowle (12) from an examination of the records in the British Columbia Game Department was able to show marked fluctuations in numbers of blue grouse in the province since about 1904. In the same study, Fowle censused blue grouse in the Quinsam area in late June and early July of 1943 and at that time found a population density of approximately 0.15 adult males per acre. The difference between this density and the density of adult males recorded in the present study is large and cannot be explained by sampling techniques alone. If the population at Quinsam Lake was truly cyclic then the density of males in 1943 should be comparable to their density in 1953. This is not the case. However, the population might fluctuate rhythmically with different "highs" at 10 year intervals. If we assume 1948 as a "low" year with a density of 0.15 males to the acre (or anything lower) then the population of 1950 recovering from this low should have been at most about 0.5 that of the "high" in 1953. Such a change did not occur. Apparently then, the Quinsam population has not conformed to a 10 year cycle. This may be explained by one of two hypotheses. (i) The present "burn ecology" of the blue grouse does not result in population cycles. (ii) Fluctuations in populations of blue grouse are not cyclic.

With the census data of 1943 and 1950 to 1953 at hand it seems logical to think of these values as points in the logistic curve. The Quinsam area was burned in 1938. By 1943 the blue grouse had begun to respond to the favorable environment with a density of approximately 0.15 adult males to the acre. At some point in population growth disease and other environmental factors began to act as controls. By 1950 an asymptote to population growth was reached at 0.40 adult males to the acre.

How this explanation fits into the provincial picture drawn by Fowle is a question. If both situations are true it would suggest that the behavior of local populations cannot be inferred from the behavior of a population treated as a province wide entity. Indeed, that the present population is

stable as a result of surviving young replacing loss in the older age classes indicates the local nature of this blue grouse population and in turn the local nature of its environmental controls. What the distribution of this environmental complex might be is a question. On the other hand, the densities of grouse observed in 1943 and between 1950 and 1953 at Quinsam Lake may be part of a long term fluctuation either local or province wide. The results of future censuses should answer this question.

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